IMPERIAL AGRICULTURAL
RESEARCH INSTITUTE, NEW DELHI.

MGIPC—S4—III-1-93—22-8-45—5,000.

THE AMERICAN NATURALIST

THE SCIENCE PRESS PRINTING COMPANY
LANCASTER, PENNSYLVANIA

THE
AMERICAN NATURALIST

EDITED BY JAQUES CATTELL

A BI-MONTHLY JOURNAL
DEVOTED TO THE ADVANCEMENT OF THE BIOLOGICAL SCIENCES
WITH SPECIAL REFERENCE TO THE FACTORS OF EVOLUTION

VOLUME LXXVIII

LANCASTER, PA.
THE SCIENCE PRESS
1944

THE
AMERICAN NATURALIST

Vol. LXXVIII *January–February, 1944* No. 774

THE PROBLEM OF SPECIES IN OENOTHERA[1]

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It is altogether fitting that the seventy-fifth anniversary of the founding of the oldest biological journal in the United States should be celebrated by the country's oldest general biological society. It is not merely similarity in age, however, that makes this a fitting celebration: it is rather the fact that THE AMERICAN NATURALIST and the American Society of Naturalists, although independent in origin, and at no time in their long history organically connected, have had common interests and ideals and have tended to emphasize the same aspects of the broad field of biology. The society and the journal have both been characterized by breadth of viewpoint and by an emphasis upon those aspects of biology which are the common concern of all students of the life sciences, whether they be botanists or zoologists. They have thus served as a unifying influence during a period when the biological fraternity has tended to break up into a multitude of isolated and often mutually exclusive groups. The society takes this opportunity to felicitate the journal, therefore, upon seventy-five years of brilliant service to the whole of biology, and to congratulate it upon the high level of excellence which its pages have maintained, and upon the influence which it has exerted upon the development of biology and the unification of biologists. It extends its best wishes for a long and equally brilliant career in the future. It is happy that it now shares in the responsibility for maintaining the high excellence of the journal through a board of advisory editors chosen by the society. It is to be hoped that the journal and the society will cooperate for many years to come in the furtherance of those aims and ideals which all biologists hold in common.

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[1] Presidential Address, American Society of Naturalists, December, 1942. The program of this meeting was planned in celebration of the seventy-fifth anniversary of THE AMERICAN NATURALIST. The meeting, which was to have been held in New York City, was cancelled at the last moment at the request of the Office of Defense Transportation. The work reported in the paper has been supported in its earlier stages by the Penrose Fund of the American Philosophical Society and in recent years by the Rockefeller Foundation.

In view of the predominant interest of both THE AMERICAN NATURALIST and the American Society of Naturalists in the study of organic evolution, it seems appropriate that I should select a subject dealing with this general field of study. I have, accordingly, chosen to speak upon "The Problem of Species in *Oenothera*."

The genus *Oenothera* is a large and varied assemblage, which ranges widely over the Western Hemisphere. If we adopt the classification of Munz (1928–1938), it includes fifteen subgenera. All these are found in North America, ten of the fifteen being confined to this continent. Five subgenera (*Sphaerostigma, Lavauxia, Hartmannia, Raimannia* and *Euoenothera*[2]) extend down into South America, some forms reaching the southern extremity of Argentina and Chile. Of the subgenera confined to North America, six are restricted almost wholly to regions west of the Mississippi River, being especially abundant west of the Rockies. Only four subgenera (*Calylophis, Raimannia, Kneiffia* and *Euoenothera*) reach the eastern states. Very little is known in regard to the cytogenetics and the phylogenetics of most of these subgenera. Schwemmle and his students (1927–1939) have done some work on *Raimannia* and *Hartmannia*, and a few minor cytological observations have been made on other subgenera. With these few exceptions, however, all the extensive cytogenetic work on *Oenothera* has been confined to the North American forms of the subgenus *Euoenothera* and to certain European races of this subgenus which have been introduced into that continent from North American sources. The situation which has been found to exist in this subgenus, however, is so unusual that it is highly desirable that the other subgenera be investigated also with comparable thoroughness. A beginning is being made in this direction at the present time, the results of which will be mentioned later.

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[2] Dr. Munz informs me that the term *Onagra* should be supplanted by the term *Euoenothera*. I am consequently using the latter term in this paper.

It is not my purpose to discuss in detail at this time the peculiarities of the cytogenetic behavior of *Euoenothera*. These are already well known to most biologists. I wish rather to show how these peculiarities have led to an unusual taxonomic situation and how it has been possible to acquire an understanding of the essentials of this situation as a result of cytogenetic analyses. I will deal first with the North American euoenotheras, and later will briefly compare the situation found in this group with that found in the South American members of this subgenus and other subgenera.

Taking up the North American euoenotheras, then, it is first necessary to emphasize the fact that those found in California, Northern Mexico and contiguous areas differ in their cytogenetic behavior from those which grow farther east and north, in that they do not show in any marked degree the peculiarities which characterize the North American euoenotheras as a whole. They have for the most part paired chromosomes in meiosis and they lack lethals. The taxonomic problems raised by these plants are not, therefore, in essence different from those raised by other groups with "normal" cytogenetic behavior.

As one proceeds eastward, however, the cytogenetic behavior of the group gradually changes. In the races found in Arizona, New Mexico and Utah, for instance, the chromosomes show a considerable tendency toward circle-formation, so that a large proportion of a given population, or all of it, will show circles of intermediate size in meiosis. Such configurations as ⊙ 6,[3] or ⊙ 8, or ⊙ 10, or ⊙ 4, ⊙ 6 have been found in most of the plants studied. In a few cases, the chromosomes in these circles seem to have acquired lethals, so that lethal systems, either balanced or unbalanced, have been set up. In other cases, no evidence of lethals has been obtained, and the plants do not breed true to the presence of circles, throwing in each generation a proportion of plants with wholly paired chromosomes, or with only one circle instead of two.

As we proceed still farther eastward and reach the Rocky Mountain region of Colorado, or as we go northward into Washington, we find that practically all plants have a circle of 14 chromosomes in meiosis. This circle carries, almost without exception, a balanced lethal mechanism, so that the plant, which is generally self-pollinating, breeds true for the circle. More than 120 races from the Rocky Mountains and from those parts of the United States and Canada which lie eastward from this region have been examined cytologically by the present author and all but six of these have shown a circle of 14 chromosomes in meiosis, and balanced lethals. It is this great assemblage of circle-bearing and lethal-bearing races which constitutes a taxonomic puzzle which has hitherto defied the efforts of those who have tried to classify them.

That the taxonomic situation within this assemblage is indeed puzzling soon becomes apparent to any one who attempts to study it. All students of *Euoenothera* recognize that multitudinous forms and races exist within the subgenus, but when one attempts to place them in separate categories which might reasonably be called species, one finds himself in difficulties. Thus, Dr. Charles C. Deam, one of our ablest taxonomists, remarks in his "Flora of Indiana" (p. 705): "The plants are exceedingly variable and only an expert can name them with any degree of certainty. I have a large number of specimens which I am not including in this treatment because I cannot satisfactorily name them.'' The result of this situation is that the taxonomists have had to classify the group in a manner which they themselves regard as highly unsatisfactory. Thus, in Gray's Manual we find only five species and one escape recognized which would belong to *Euoenothera.* In Deam's ''Flora of Indiana,'' four species are listed which belong in this subgenus. And yet all taxonomists realize that the situation is not as simple as this—that the small number of species recognized does not take into account the enormous variety which exists in the subgenus. It is the best that can be done, however, with purely taxonomic methods.

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[3] The symbol ⊙ means "circle of."

The difficulties which confront the taxonomic student of this group owe their existence to certain peculiarities of behavior which will now be explained under four headings.

(1) The euoenotheras which range from the Rockies eastward exist in the form of numerous locally distributed geographical races, which, because of their self-pollinating habit, are more or less effectively isolated from one another. It is because of the presence of these races in such large numbers and the fact that they differ from each other oftentimes in but minor characteristics that the heterogeneity so disconcerting to the taxonomist is introduced into the population as a whole. This heterogeneity is due to a multiplicity of races, and not to variation within the individual races. Each race is made up of self-pollinating individuals, and the race breeds true to a degree rarely attained elsewhere in nature. It is not too much to say that the progeny of a given plant are ordinarily identical with this plant from the genetic point of view. This lack of variability within a race, which contrasts so strikingly with the variability found in the population as a whole, is not a result of homozygosity, for these plants are far from being homozygous—they are often notably heterozygous. It is due rather to the pres-

ence of a circle of 14 chromosomes in which balanced lethals are present. The separation of adjacent chromosomes in the circle into different germ cells produces but two kinds of gametes, genetically speaking, which are identical with those contributed originally to the plant through sperm and egg. The lethals compel recombination of these in selfed line and hence produce plants identical with their parents, except for the results of whatever crossing-over may occur between associated complexes. Crossing-over is apparently a factor of minor significance in *Euoenothera,* however, being probably confined for the most part to the pairing ends, and its occurrence does not alter appreciably the true-breeding character of each race. Each race, therefore, is almost as uniform genetically as a clone, although successive generations are sexually produced. Furthermore, since each race is self-pollinating, a considerable degree of isolation is maintained between races. The first fact of importance, therefore, in an understanding of the taxonomic situation, is the existence of a great variety of true-breeding geographical races or biotypes, each more or less isolated by reason of its self-pollinating habit from other races.

(2) The second point is the fact that the isolation between races is not absolute. The barriers due to self-pollination can be overcome and are overcome from time to time. It has been found that sterility barriers do not exist between the various races of the North American euoenotheras. When artificially crossed, any race is able to form fertile progeny with any other race, the only exceptions being cases where plasma incompatibilities exist. In the field it has been noticed that insects often enter unopened buds in search of pollen and where they bring foreign pollen to a bud, or an open flower, whose anthers have failed for some reason to produce abundant pollen, it is probable that cross-fertilization takes place.

When such crosses occur, the hybrids which result appear to undergo a form of natural selection by which practically all hybrids which do not possess a ⊙ 14 are eventually weeded out. As I have pointed out elsewhere

(1940), ⊙ 14 probably has a sufficient survival value in comparison with other configurations to ensure its perpetuation at the expense of forms possessing some other configuration, since plants possessing this configuration will have a maximum of hybrid vigor coupled with abundant reproductive capacity resulting from the certainty of fertilization that goes with self-pollination. Furthermore, plants with ⊙ 14 require only a single pair of balanced lethals to enable them to breed true to this configuration, whereas plants with more than one circle would require balanced lethals in each circle if they were to breed true to their configurations. Since hybrids with ⊙ 14 are self-pollinating, and since they have balanced lethals and are able to breed true in respect to their configuration, there is no reason why they should not become the progenitors of new geographical races, each maintaining the same degree of isolation as is maintained by its parent race.

(3) The third factor in the taxonomic situation to be emphasized, therefore, results from the second. It is that new races may come into existence by hybridization, whenever the barrier between races is broken down by accidental cross-pollination, and a hybrid with ⊙ 14 and balanced lethals results. That this is a way in which new races are formed in *Euoenothera* is not mere surmise. The following facts seem to point to hybridization as a factor of prime importance in the origin of new races in this subgenus.

First, the complexes[4] which are associated to form a

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[4] The term "complex," as used by the present author, has a somewhat broader meaning than the term "genome." It refers to a haploid set of chromosomes having a specific segmental arrangement as well as a definitive set of genes. If a complex becomes either segmentally altered or genically altered, it is no longer the same complex. Thus, *gaudens* (of *lamarckiana*) and *rubens* (of *biennis*) are identical segmentally, but not identical genically. They are, therefore, different complexes. On the other hand, the *albicans* of *biennis* and the *albicans* of *suaveolens* are identical segmentally, and essentially identical genically. The same complex is, therefore, considered to be present in these two races. If any cases were found where genic identity was accompanied by segmental diversity, it would be considered that two different complexes were also involved.

given race are not only dissimilar in segmental arrangement: they are frequently very diverse in genetic composition, as is shown by the diverse phenotypes which they produce when outcrossed to other forms. The fact that associated complexes are not closely related to each other cytologically or genetically strengthens the assumption that they represent diverse lines of evolution which have been brought together by outcrossing.

A second significant fact is the great similarity which exists between complexes of different races. Thus, while a given complex differs profoundly from the complex with which it is normally associated to form a plant, it may be identical in segmental arrangement and genetically similar to or identical with complexes in other races. We have turned up a number of cases where complexes with identical segmental arrangements exist in widely scattered races, being associated in one race with one complex, in another race with an entirely different complex. In most of these cases these cytologically identical complexes are also very similar to each other genically, while at the same time they are, in some cases, very different from the complexes with which they are associated. It is difficult to understand how a given complex can exist in more than one race, being associated with different complexes in the different races of which it is a part, unless this situation has been brought about by hybridization. A given race, with this particular complex, has crossed at various times with various other races, thus establishing a variety of new races carrying one complex in common. In all probability most euoenotheras with ⊙ 14 trace back to a hybrid origin, some complexes surviving in two or more true-breeding races thus formed.

It should be admitted, however, that some races may trace back only indirectly to a hybrid origin, for there exists the possibility that the complexes in a given race may become altered in one way or another in the course of time. For instance, interchanges may occur between associated complexes. Since the two complexes in a plant are usually so diverse, an interchange between them may more or less profoundly change their genic and possibly their segmental characteristics. Such an interchange may be in the nature of crossing over in the pairing ends, which will not alter the segmental arrangements of the chromosomes making up the complexes; or it may involve reciprocal translocation between chromosomes of opposing complexes, which will alter the segmental arrangements of the complexes and thus create complexes which are new cytologically as well as genetically. It is also possible for an interchange between two chromosomes of the same complex to bring about an exchange of genes between the two associated complexes and the creation of cytologically and genetically new complexes (Cleland, 1942). In addition to these methods of alteration, there is also the possibility of the occurrence of point mutations. Because of the presence of balanced lethals, any recessive mutations which occur may be carried on from generation to generation indefinitely and will tend to accumulate to a point where the complex has become distinctly altered genetically.

There are ways, therefore, by which complexes can be altered. They can become altered in respect to genic composition while still retaining their own segmental arrangements. They can become altered both genically and in segmental arrangement. Thus it comes about that, while complexes in different races which are closely related from the standpoint of segmental arrangement are usually similar genetically, some exceptions are found. All this tends to complicate the situation somewhat—to increase the number of segmental arrangements existing in nature, and to break down to some extent clear lines of distinction between complexes of different ancestries and origins. It also results in occasional segregation of new types from old races, through the creation of gametes with new genetical and/or cytological characteristics. Some plants receiving the altered complexes may have less than ⊙ 14 and are not likely to survive, but others may still have ⊙ 14 and thus be capable of giving rise to new true-breeding races which may carry new combinations of genetic and phenotypic characteristics. When one contemplates the possibilities of interchange that exist between associated complexes, and of genic alteration through the accumulation of point mutations, the wonder is that the situation in nature is not more complicated than it is. The fact that it is not more complicated indicates, in all probability, that these genetical and cytological alterations occur at the most with only moderate frequency.

(4) A fourth factor which influences the taxonomic situation is the fact that a majority of the dominant genes in a plant may be carried by one of the complexes, in consequence of which the phenotypic effect of the other complex is completely or almost completely hidden. There are many cases where this is so. Many of the broad-leaved "*biennis*"-type races carry a complex producing narrow-leaved *strigosa*-like plants when outcrossed to the proper race, as well as a complex producing broad-leaved plants. Other broad-leaved races do not carry such a complex, both of their complexes producing broad-leaved plants. It is very difficult, if not impossible, however, by mere external examination of a broad-leaved race to tell to which of these two categories it belongs—whether it carries a *strigosa*-like complex or not.

We can now see why it is that the task of determining relationships in the euoenotheras east of the Rockies becomes a difficult one from the purely taxonomic standpoint. This group is not made up of species in any sense in which this word is ordinarily used, and such entities as do exist do not lend themselves to classification by taxonomic methods. If we may summarize the facts just discussed, we will have a clearer picture of the sorts of entities which do exist:

(1) The population consists of a multitude of true-breeding races, often occupying the same area, but more or less isolated from each other because of their self-pollinating habit.

(2) Each race is a complex-heterozygote, containing two complexes which differ from each other in segmental arrangement and which are often very diverse genetically.

(3) These races are of hybrid origin, stemming from the infrequent occasions when the reproductive barriers have been transgressed; or they have been derived from such hybrid races as a result of modifications in genetic constitution or in segmental arrangement, which have followed gene mutation, crossing over or reciprocal translocation.

(4) One complex in a race is often masked by the other, so that its presence cannot be detected except by appropriate out-crosses. Hence, the relationships which a plant has through the masked complex will not be recognized unless such crosses are made. Nor can races which carry such hidden complexes be distinguished by external examination from those which do not.

It is evident that the groups which have the best claim to be considered valid taxonomic entities are the multitudinous geographical races which make up the general population. Should these be considered species? They have a degree of distinctness in that they do not ordinarily cross with other races. This is not, however, as clear-cut a barrier as exists in many other genera, for any race of North American *Euoenothera* is capable of crossing with any other, and of producing fertile progeny. The isolation which is maintained is due to the mere mechanical factor of self-pollination, and is in no sense as perfect as, let us say, in the case of the various species of *Drosophila*. When one couples this with the fact that these races are often too similar in appearance to be readily distinguishable and that they are so numerous, one begins to question the justification of calling such races "species." They are biotypes to which one might apply the term "microspecies," but they are certainly not the sorts of groupings with which the taxonomist can readily work. We are forced to conclude that, if there are no other groupings which can be called species in the population, the term "species" should not be used in connection with this assemblage at all. Are there, then, any other groupings which might conceivably be called species?

There is indeed some evidence of larger groupings, but, while some of these might possibly be handled with some degree of satisfaction by the taxonomist, others could not be so handled. I will briefly review our present knowledge of these larger groupings.

We shall confine our attention to the euoenotheras ranging from Colorado eastward. Those to the west and south of this region have more or less normal cytological and genetical behavior and do not constitute a taxonomic problem too different from that found in other genera.

In general, we find that the western plains area is dominated by an assemblage of forms which have thick, narrow to moderately narrow, greyish green, and relatively uncrinkled foliage. This may be called tentatively the *strigosa* assemblage. This is replaced to the east by a plexus of plants with broad, crinkled, thin, clear green foliage, to which a variety of names has been applied, such as *biennis, pycnocarpa, nutans* and *laevigata.* In the southeast, along the Gulf Coast and spreading northeastward are plants with narrow, but dark, thin, clear green leaves which we may call the *grandiflora* assemblage, although most of them have flowers of moderate size. In the north-east, one finds a variety of forms which have very narrow, greyish or dark green leaves, with appressed or obsolete pubescence. The stems of these plants bend downward, then upward, at the tips in a characteristic fashion, and the buds have subterminal sepal tips. These may be referred to tentatively as the *parvifloras.*

While too few races have been studied for us to say definitely to what extent these groups grade into one another, or to what extent they are distinct, our impression is that the *strigosas* are fairly distinct from the *biennis* types, phenotypically, and the *parvifloras* are likewise reasonably distinct. The *grandifloras,* however, seem to grade rather insensibly into the broad-leaved types. It will be interesting to ask how these different groups behave cytogenetically, whether the individual races within a given larger group have common cytogenetic features, whether the races in different larger groups differ cytogenetically, and whether any evidence of the existence of relationships between larger groups is obtained from cytogenetic studies.

Some seventeen races belonging to the *strigosa* assemblage have been studied in considerable detail, and it is found that there is considerable homogeneity in cytogenetic behavior in the group as a whole. Without going into detail, the following points characterize all the races so far analyzed. Each race has ⊙ 14 and balanced lethals. The complexes in a given plant produce similar phenotypes and may be rather similar genetically. One complex is transmitted through the egg (the α complex), the other through the sperm (the β complex). When these races are crossed out to the hookeris from California, either as male or female parent, hybrids with intermediate-sized circles are produced, indicating that both α and β complexes are removed by only three or four interchanges from the commonest *hookeri* end arrangements. Since the α complexes from different *strigosa* races can not be combined with each other as a rule, being transmitted only through the egg, nor can the β complexes, which are transmitted as a rule only through the sperm, it is not usually possible to obtain hybrids between two alpha or two beta complexes, but it has been possible to work out the segmental arrangements of quite a number of complexes in terms of certain defined standards, and it is found that the α complexes are very similar to each other in segmental arrangement, and the β complexes are also very similar to each other. In fact we have one case where two α complexes in different races are identical in segmental arrangement (both from Iowa), and we have two cases where two β complexes are identical (one case of identity being between a complex from Colorado and one from North Dakota, the other being between one from Colorado and one from Nebraska). An analysis of the segmental arrangements of the various complexes shows an entirely different history of interchange behind the α complexes on the one hand and the β complexes on the other. The α complexes are all very similar to one another in respect to the interchanges which have produced them; the β complexes also show close similarities, but there are no cases known where interchanges have occurred between the same chromosomes in the formation of α and β complexes. It is evident that the α complexes have had a similar and perhaps a common origin and the β complexes have also had a common origin, but one different from that of the α complexes. It is probable that the strigosas represent the results of crossing between two overlapping and independently developed populations, one of which may have migrated into the region from the west coast, the other having spread northward from Mexico. Where the populations overlapped, crosses occasionally occurred and true-breeding hybrids were established which were the progenitors of present-day strigosas.

If this surmise is correct, it is probable that, in one sense, the strigosas have had only indirectly a common origin. Many crosses probably took place in different localities and the present-day strigosas probably stem from many independent crosses rather than from one. While they are alike in having arisen from the same two ancestral populations, they trace their ancestry back to a variety of independent beginnings. It is quite probable that the original populations were not entirely homogeneous cytogenetically and that the various strigosas were in some cases somewhat unlike in segmental arrangement and in genetic composition when they were first formed. The similarity between the various α complexes, however, which are presumably derived from one of the parental populations, and the similarity between the various β complexes, which are derived from the other parental population, do not allow us to assume any very great amount of heterogeneity in the races which crossed to produce the strigosas.

Turning now to the broad-leaved races, we find again more or less clear-cut types of cytogenetic behavior, but these are, unfortunately for the taxonomist, not clearly correlated with differences in external appearance. From the standpoint of cytogenetic behavior these races fall into three groups, but it is not possible at present to tell with any degree of certainty to which group a given plant belongs by looking at it, since the plants are all broad-leaved and more or less similar in appearance. Up to the present time, 21 races have been studied belonging to group 1, 12 races belonging to group 2, and 4 races belonging to group 3. Much of the work on these forms has been done by Dr. Bayard L. Hammond and by Mrs. Louise Brandau Preer. In group 1, the α complexes carry genes for broad leaves and other so-called "*biennis*" characters, the β complexes carry genes for an essentially *strigosa*-like set of characters. In group 2, the α complex carries genes for *strigosa*-like characters and the β complex carries genes for "*biennis*" characters just the reverse of the situation in group 1. In group 3, both complexes are of the "*biennis*" type, producing broad leaves in outcrosses. In group 1, the α complexes closely approach the complexes of the *hookeri* alliance from the standpoint of segmental arrangement. In one race, the α complex has an arrangement identical with that of the commonest (ancestral ?) *hookeri* arrangement (that of ʰ*Johansen*, etc.) ; in eleven races, its arrangement differs from this putative ancestral arrangement by but one interchange; in five races, its arrangement differs by a minimum of three interchanges. The β complexes of group 1, on the other hand, differ decidedly from the hookeris in segmental arrangement. None of those studied could have been derived from the ʰ*Johansen* arrangement by less than three interchanges (one race), and most of them are more distantly related to this complex, differing from it by a minimum of four interchanges (two races), five interchanges (nine races) or six interchanges (three races). In group 1, then, the α complexes carry genes for "*biennis*" characters and are close to the hookeris segmentally; the β complexes carry genes for *strigosa*-like characters and are far-removed from the hookeris segmentally.

In group 2, a complex carrying genes for *strigosa*-like characters is again associated with one carrying genes for "*biennis*" characters, but in this case, the former is the α complex and the latter is the β complex. With respect to segmental arrangement, the situation is not quite so clear-cut as in the case of group 1. The α complexes differ from the *Johansen* arrangement by a minimum of one (one race), two (one race), three (six races), or four (two races) interchanges; the β complexes differ by a minimum of three (four races), or five (six races) interchanges. In all cases where one complex is farther removed from the hookeris than its associated complex, it is the β complex which is farther removed. In group 1, it is also the β complex which is farther removed, but in group 1 the β complexes are the narrow-leaved ones, whereas in group 2 they are the broad-leaved ones.

In group 3, both α and β complexes carry genes for broad leaves and other "*biennis*" characters, and both complexes are moderately close to the hookeris in segmental arrangement, differing in all cases so far studied by a minimum of only two or three interchanges. It is as though the plants of this group were made up of two complexes similar to the α type in group 1 or to certain of the β type in group 2.

The three groups just characterized can not be distinguished from each other phenotypically with certainty. We are inclined to feel that we could, in a fair number of cases, pick out the wild races which carry two broad-leaved complexes (group 3), if they were brought into our garden, but we would find considerable difficulty in distinguishing between the other two groups. There is, however, a certain correlation between this grouping and geographical distribution. The group 1 races which we have studied were found for the most part in the Middle West, some of them, however, being found in the East. The following states are represented by this assemblage:

Arkansas, Missouri, Iowa, Illinois, Indiana, Kentucky, Maryland, Virginia. Group 2 races have come largely from the Northeast, the following states and provinces being represented: New Brunswick, Quebec, Ontario, Wisconsin, Michigan, New York, West Virginia, North Carolina. Group 3 has been found only in Virginia and North Carolina. It may be that the group 1 population has spread eastward from the Middle West, that the group 2 population has spread southward from the Northeast, and that these populations have overlapped in the region of Virginia and the Carolinas, resulting in the production of group 3 plants in this area, each carrying an α complex from group 1 associated with a β complex from group 2.

I referred earlier to the fact that complexes with the same segmental arrangement may exist in different races and that this is one indication of the hybrid origin of these races. We saw that there are some cases of this in *strigosa*. We have more striking cases among the broad-leaved forms. In group 1, there is one segmental arrangement which is so characteristic of the α complexes that it may prove to be more or less typical. This segmental arrangement exists in the α complex of nine of the twenty-one races so far studied. These nine races are found in Maryland, Kentucky, Indiana, Missouri and Arkansas—in other words, this segmental arrangement is widespread geographically.

Five of these nine races have β complexes which differ from one another in segmental arrangement. The other four races, residing in Maryland and Kentucky, have β complexes which are identical in segmental arrangement. Four races, therefore, are identical in the segmental arrangement of both complexes. It is interesting to note, however, that these races are quite easily distinguishable phenotypically. It is probable that genic changes not affecting segmental arrangement have occurred in their complexes since the time when the last alteration in segmental arrangement occurred, causing them to diverge from one another genetically, while still retaining identical segmental arrangements.

In addition to these cases, several other cases of identity or near identity are known among the broad-leaved forms. It seems clear that the actual number of segmental arrangements is somewhat fewer than the number of races, some arrangements being found in more than one race. This serves to emphasize the probability that the various races have come into being through a process of hybridization.

With respect to the cytogenetic behavior of the *grandiflora* assemblage and the parvifloras little can be said as yet. The grandifloras grade to such an extent into the broad-leaved assemblage that no clear-cut line of demarcation has as yet been recognized. Cytogenetically all races so far examined have ⊙ 14 and balanced lethals. The complexes in any given race produce similar phenotypes—often distressingly similar, but one of them is close, or very close, to the hookeris segmentally, the other far removed not only from the hookeris but from every other complex so far analyzed. While only a few grandifloras have been examined, this general picture seems to characterize those which have been studied. Much more work will have to be done on the group, however, before it can be characterized with certainty.

The parvifloras are being studied by one of my students, Miss Lucie-Blair Hodges, but the work has not progressed far enough for definitive results to be announced. In general, the parvifloras, while differing greatly among themselves, seem to be fairly clearly demarcated from other groups. They all have ⊙ 14 and balanced lethals. In general they appear to have β complexes which produce bent stem tips and subterminal sepal tips, and which, when outcrossed, prevent the plastids of most other groups from developing chlorophyll. The latter characteristic makes it difficult to obtain hybrids between the β complexes of the parvifloras and complexes from other groups. Hence it will be difficult to determine their segmental arrangements. The α complexes do not show a very close affinity segmentally to the *hookeri* alliance, but on the other hand they are not too far removed either. It is too early as yet to say more about their cytogenetic behavior.

From this brief survey, it is evident that the question which we raised, as to whether groupings exist which are larger than the numerous true-breeding biotypes, must be answered, with some reservation, in the affirmative. There is evidence of the existence of larger groupings with more or less distinctive cytogenetic behavior. If these groupings could be readily distinguished, the one from the other, on the basis of external appearance, there would be little objection to calling them species. The difficulty is that these groups can not in all cases be distinguished from one another. The grandifloras seem to merge insensibly into the broad-leaved assemblage, and the latter is made up of cytogenetically distinctive groups which are very difficult to distinguish phenotypically. It must be admitted that most of these larger groupings can not be handled with any degree of satisfaction by the taxonomist. We are forced to conclude, therefore, that the euoenotheras which reside from the Rocky Mountains eastward (and this constitutes the bulk of the North American euoenotheras) do not lend themselves, on the whole, to satisfactory taxonomic treatment. The larger groupings have for the most part vague and uncertain boundaries, and the multitudinous true-breeding and more or less isolated biotypes, most of which are with difficulty distinguished from their neighbors even in the experimental garden, are not the material upon which a satisfactory system of classification can be built. The best that taxonomists can hope to do is to create for convenience's sake a few categories which approximate as nearly as possible to the larger groupings which cytogenetic studies show to exist, admitting that these will in some cases only vaguely correspond to the phylogenetically significant groupings which actually exist in nature.

It would seem wiser for taxonomists to adopt this conservative policy than to follow the procedure which has in some cases been adopted, namely that of giving specific rank to every biotype which enters the experimental garden, if it happens to look a little different from other biotypes previously observed by the grower. There are too many such biotypes to give each one a specific name, and giving names to the few which are brought under observation will tend to blind one's eyes to the existence of multitudinous forms which have not yet been studied, but which have as much claim to specific rank as those already named. It would be better to admit the unique difficulties in the situation and to adopt the simplest possible system of classification, admitting that clear-cut species in the usual sense of the word hardly can be said to exist in this group and that whatever system is adopted is bound to be but an approximation to the truth.

But while this situation can not be characterized as other than highly unsatisfactory from the standpoint of the systematist, it is of undoubted interest to the student of evolution. Here we have a group, apparently of recent origin, which has developed to a high degree a unique combination of characters—chromosome catenation, balanced lethals and self-pollination—constituting a mechanism which has profoundly affected the evolutionary development of the group. On the one hand a unique opportunity has been afforded for the accumulation of recessive mutations, including lethals, and these have probably accumulated in considerable numbers by this time. On the other hand, reproductive barriers have prevented to a large extent the mingling of genes which otherwise would have become distributed more or less widely throughout the population and would have given rise to diverse genic combinations with more or less survival value. Even when crosses have occurred, the resultant genic mingling has been limited, since for the most part only hybrids with ⊙ 14 have survived, and genic segregation has not taken place to a large extent within such true-breeding types. It is perhaps not too far from the truth to say that the existent mechanism is such that it discourages the production of inter-racial hybrids, but when these are produced, those with ⊙ 14 tend to be perpetuated indefinitely, free from Mendelian segregation. Thus there has come to be a great diversity of types, but a different kind of diversity from that ordinarily found in freely interbreeding populations. Evolutionary progress in *Euoenothera* has followed and must continue to follow a somewhat different path from that pursued by other actively evolving groups.

In conclusion, it will perhaps be of interest to say a word about the cytogenetic situation in the South American euoenotheras and in other subgenera. So far as I am aware no cytogenetic work has been done hitherto on the South American euoenotheras. Through the kindness of Dr. Munz we have received seed of fifteen races of *O. campylocalyx,* one race of *O. elongata* and three races of *O. rubida.* One of my students, Mr. Charles W. Hagen, Jr., has been working on these and finds that this group shows many of the peculiarities found in the North American euoenotheras. The situation in these races may be very briefly summarized as follows:

(1) All races have shown fourteen chromosomes. Several chromosome configurations ranging from ⊙ 14 to seven pairs have been found; the situation seeming to be comparable to the situation in North America in that the majority of races have large circles, and most of the rest have seven pairs. Only one race out of nineteen has shown an intermediate configuration (⊙ 6, 4 pairs).

(2) Gamete lethals have been found in two strains, and balanced zygote lethals are present in all races with large circles. Races with large circles are in general self-pollinating, and those with seven pairs are open-pollinated, as in the North American euoenotheras.

(3) The strains classified as *campylocalyx* are extremely varied phenotypically. On the one hand, some bear a resemblance to *O. rubida;* on the other hand, some are close to *O. elongata.* It is probable that extensive investigation will show the same lack of clear-cut species that characterizes the bulk of the North American euoenotheras.

(4) The South American euoenotheras cross with great difficulty with the North American members of this subgenus. Successful crosses have been made with *O. affinis* (*Raimannia*) and it is possible that the South American euoenotheras are in reality more closely related to

> the South American Raimannias than to the North American euoenotheras.

Mr. Hagen has also made a cursory cytological examination of certain other subgenera. He finds large circles in *Hartmannia* and *Lavauxia.* Small circles or wholly paired chromosomes are also found in races belonging to both groups. Little is known as yet of the genetic behavior or taxonomic peculiarities of these subgenera.

Another student, Dr. Adolph Hecht, has made a preliminary study of the subgenus *Raimannia,* having examined a total of 53 races involving 14 of the 19 listed species, the seed for which was kindly furnished by Dr. Munz. In *Raimannia,* the species seem to be more clearly delimited than in *Euoenothera.* There is, however, considerable variability within species, numerous geographical races being present. The cytological peculiarities found in *Euoenothera* are also present in *Raimannia,* but not in so striking a degree. About 64 per cent. of the races examined have had ⊙ 14, and about 26 per cent. have had seven pairs, the remaining 10 per cent. showing intermediate configurations. Within a given species quite a variety of configurations may be present, ranging from ⊙ 14 to seven pairs. Balanced lethals are apparently present in the forms with large circles. While the analysis has not proceeded far enough to make possible definite conclusions, it is probable that there has been less of a tendency toward the production of biotypes isolated by reproductive barriers, such as are found in *Euoenothera,* since self-pollination is not so widespread a phenomenon. The evolution of the Raimannias partakes less of the peculiarities of the euoenotheras and appears to follow a more conventional pattern. The details of this situation have not been worked out as yet, however.

From this extremely preliminary excursion into the cytogenetics of other groups of the genus *Oenothera* it is apparent that the cytogenetic peculiarities found in *Euoenothera* are not confined to this subgenus alone, but are more or less widely distributed among the other subgenera. They are also found in certain other genera of the family Onagraceae. Whether any other group carries these peculiarities to such an extreme as do the North American euoenotheras, however, remains to be seen.

SUMMARY

Except for those forms growing in the southwestern portion of the United States and contiguous areas, the North American euoenotheras do not show a clear-cut segregation into readily recognizable species. Instead, the population consists of a multitude of geographical races which because of balanced lethals breed true, and because of a self-pollinating habit maintain a considerable degree of isolation from each other.

Each race is a complex-heterozygote, whose two complexes differ from each other both in segmental arrangement and in genic composition.

These races are of hybrid origin, owing their origin to the infrequent occasions upon which the reproductive barriers have been transgressed; or they have been derived from such hybrids through subsequent alteration in segmental arrangement or in genetic composition.

One complex in a race often masks the phenotypic effect of the other complex, so that the presence of the latter, and the relationships which this race bears through the latter, can only be shown by outcrosses.

These races fall on the basis of cytogenetic behavior into larger groups. These are the comparatively narrow-leaved forms of the western plains area, the middle-western broad-leaved forms, the north-eastern broad-leaved forms with difficulty distinguishable phenotypically from the middle-western ones, a third broad-leaved group found in Virginia and North Carolina, the grandifloras of the southeast coastal plains area and the parvifloras of the north-east. These groups can not always be distinguished from each other with any degree of certainty on the basis of phenotypic characters and, hence, are of little value to the systematist. They show distinctive cytogenetical behavior, however, and constitute the nearest approach to species in the usual sense of the word to be found in the assemblage.

The major factors which have brought about this situation have been (in addition to gene mutation) segmental interchange leading to circle formation, the development of balanced lethals, the acquisition of a self-pollinating habit resulting in the erection of reproductive barriers between races, and the occasional transgression of these barriers through outcrossing leading to the origin of new races. Evolutionary progress in this group has, therefore, followed a rather different pattern from that found in other organisms.

The cytogenetic situation in the South American oenotheras, so far as this is known, is briefly summarized and compared with the situation in the North American euoenotheras.

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THE EARLY HISTORY OF THE AMERICAN NATURALIST[1]

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THE first issue of *The American Naturalist, A Monthly Magazine of Natural History,* appeared in March, 1867. It is thus sixteen years older than the American Society of Naturalists, which was organized in 1883. The relations of the society to the magazine have always been close. Its editors and associate editors have been almost invariably members of the society and two of the founders of the magazine were also founders of the society. At the third meeting of the society in Boston in 1885 THE AMERICAN NATURALIST was made the official organ of the society for publication, and so far as I can discover that act has never been rescinded. It is therefore appropriate that some important events in the history of the magazine should be brought to the attention of the members of the Society of Naturalists.

THE AMERICAN NATURALIST was started, soon after the close of the war between the States, by four men who had been students of Louis Agassiz and assistants in the Museum of Comparative Zoology at Harvard College. These men were Alpheus S. Packard, Jr., Frederick W. Putnam, Edward S. Morse and Alpheus Hyatt. All of them had been assistants in the museum for several years, and two had left to serve in the Union Army, Packard as assistant surgeon in the 1st Maine Volunteers and Hyatt as captain in the 47th Massachusetts Regiment. They were therefore men of maturity as well as enthusiastic naturalists. Their positions at the Museum of Comparative Zoology were much like those of graduate assistants in our present universities. They attended lectures by

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[1] This paper was prepared for the annual meeting of the American Society of Naturalists, which was scheduled to be held in New York City on December 29, 1942, but was cancelled owing to war conditions.

Professor Agassiz and worked on the collections in the museum, each in his own chosen field. Their relations with the professor were in general cordial, in some cases almost worshipful, but they were mature men, desirous of making careers for themselves and of becoming self-supporting. Their pay was small, and their hours long. It is known that Packard received $400 a year and the others probably similar amounts. Each of them had problems of his own which he wished to work on, but museum duties left little opportunity for independent work. Under these circumstances it is not surprising that discontent arose. Agassiz was unable to increase their pay, his own salary at the time is said to have been only $1500 a year, and he felt that his assistants should devote their working time to the museum.

The spirit of independence in the assistants reached a climax when a sheet of "Regulations for the Museum of Comparative Zoology" was posted, which was designed to prevent assistants from working on their own problems during museum hours. As a result five of the older assistants swarmed out of the museum hive; Addison E. Verrill went to the Smithsonian Institution, and later to Yale, while Packard, Putnam, Morse and Hyatt went to the old Essex Institute and the new Peabody Academy of Science at Salem, Mass. Nathaniel Shaler was urged to join them, but he declined, saying that he had just finished putting down one secession (in the Civil War) and was not going to join up with another. Packard later became professor of zoology at Brown University; Putnam professor of anthropology successively at Chicago, California and Harvard; Hyatt became curator of the Boston Society of Natural History, while Morse continued to the end of his long life as director of the Essex Institute and Peabody Academy at Salem.

Putnam was a nephew of George Peabody, a native of Essex County, who had made a great fortune as merchant and banker before moving to London and whose benefactions established Peabody Institutes in several American cities. Putnam was director of the Essex Institute from 1864 to 1870, and probably knew in advance of his uncle's intended gift to the Essex Institute, for in 1866 he had written to Morse, Hyatt and Packard that by the fall of that year they would be offered employment there. The founding of the Peabody Academy of Sciences and the starting of THE AMERICAN NATURALIST are well described by Dorothy G. Wayman in her excellent book, "Edward Sylvester Morse,"[2] from which I quote the following sentences:

> On February 26, 1867, George Peabody placed in the hands of the trustees of the Essex Institute $140,000 "for the promotion of science and useful knowledge in the county of Essex," and he provided that the Institute and the East India Marine Society be combined. Thus the Peabody Academy of Sciences came into being and in May, 1867, Morse, Hyatt and Packard became members of the staff, of which Putnam was already Director.
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> On November 22, 1866, these four men drew up an "Agreement of the Editors of THE AMERICAN NATURALIST," which begins:—"The following expenses are to be paid first and in the following succession: 1. Paper, 2. Printing, 3. Engraving, 4. Binding, 5. Incidentals, 6. Advertising, 7. Drawing, 8. Chief Editor's actual expenses for the year, board, clothing, traveling. Should any money remain after the above expenses are paid, this amount will be divided among the Editors according to the amount of their contributions pro rata." . . . Packard looked after the publishing details; Hyatt kept the books, and Morse, as secretary, had charge of the mailing list and subscriptions. Their first printing was of 250 copies. The Magazine was published [by the founders] until 1878. It never made its editors rich, but it was the first publication to combine science and popular interest and to use artistic illustrations for scientific articles. Packard wrote most of the articles, and Morse made most of the drawings . . . Putnam was indefatigable in his work for the NATURALIST, correcting proof, and finally establishing a printing office known as the Salem Press.

Although Packard was chief editor it is certainly not true that he wrote most of the articles. The first volume of 680 pages contained 47 principal articles by 39 authors (of which Packard wrote 5, Morse 2, Hyatt 1), 23 reviews of current works on natural history, 26 shorter articles or notes on botany, 38 on zoology, 11 each on geology and mineralogy, 9 pages of a natural history calendar for the

[2] Harvard University Press, 1942, pp. 211–216.

different months, 18 of correspondence and reports of the proceedings of scientific societies, and finally 8 pages giving a glossary of scientific terms used in the volume.

The introductory statement in the volume says that "The Naturalist aims to be a scientific monthly addressed to all lovers of nature; it is hoped that it will be equally welcome to farmers, gardeners, and artisans. Its aim is practical and economic as well as theoretical." Thus the Naturalist was intended to be not only a general scientific magazine but also a journal of scientific news, for at that time there was no other publication in America performing these services. Later as various technical journals were established they took over publication of much of the research work in the natural sciences, while *Science, Popular Science Monthly* (now *Scientific Monthly*) and other popular journals in various fields of science took on some of the many functions which the Naturalist initially performed.

In this process of differentiation the history of the magazine is not unlike that of the Society of Naturalists. Just as the latter gave rise by gemmation to the Association of Anatomists and to the Geological, Physiological, Morphological (now Zoological), Psychological, Botanical and Bacteriological Societies, so The American Naturalist has budded off the various journals of all these societies. The question is sometimes asked whether there is any present need for a Naturalist's Society or journal. However, in all life and development integration must accompany differentiation and there is now a growing interest in the general and philosophic aspects of science. Furthermore, there is need of a journal which specializes in the more general fields of natural history. When the question was asked, several years ago, whether there was any further work for the American Society of Naturalists, it was the general opinion that it served a very useful purpose by bringing together workers in botany, zoology, geology and the natural sciences in general and providing a forum for the discussion of problems common to all of them. One of the most general of all problems of the natural sciences is evolution, and at the Baltimore meeting of the Society of Naturalists in 1908 it was voted "that the study of evolution be the general policy of the Society, unless otherwise ordered." This "temporary plan" has now become the settled policy of the society, evolution being properly interpreted to include genetics, cytology and biochemistry, as well as the more usual fields of speciation, adaptation, distribution and in general the philosophy of the natural sciences.

In like manner the field of the journal, AMERICAN NATURALIST, has of late followed the policy of the Society of Naturalists. The symposia at the meetings of the society are usually printed in the journal and are generally of a high order of excellence. Other contributions that are published in the NATURALIST are usually of such importance that it is widely recognized as one of the leading scientific journals of America. Although it is not owned by the Society of Naturalists it is still its "official organ for publication," as it has been since 1885.

The first three volumes were edited by A. S. Packard, Jr., E. S. Morse, A. Hyatt and F. W. Putnam; volumes four and five were edited by Packard and Putnam, while Morse and Hyatt were associate editors and thereafter their names disappear from the editorial staff. Volumes six to nine were edited by Packard and Putnam, with R. H. Ward, associate editor for microscopy. With volume ten and eleven Packard alone appears as editor, with R. H. Ward and G. H. Goodale as associate editors.

The first nine volumes were published in Salem, Mass., the first by the Essex Institute and the others by the Peabody Academy of Sciences. Volumes ten and eleven bear the imprint, "Boston: H. O. Houghton and Company." The last paragraph on the last page (758) of volume eleven carries the following, "IMPORTANT ANNOUNCEMENT

TO SUBSCRIBERS. THE AMERICAN NATURALIST will hereafter be published by Messrs. McCalla and Stavely, Philadelphia, Pa., and will be edited by A. S. Packard, Jr., and Prof. E. D. Cope, with the assistance of eminent men of science."

It is evident that all the original founders and editors, except Packard, had grown weary of the editorial work and that the publishers had not found the NATURALIST a profitable venture. Under these circumstances Cope acquired ownership and undertook the business management as well as editorial supervision. Cope was not a business man nor a meticulous editor; he was too busy with scientific expeditions, writings and other matters of greater moment to pay much attention to the Philadelphia publishers, and probably Packard was too far away. The editorial policy was so generous, and the possible outlets for publication so restricted, that the monthly magazine grew to giant size, many annual volumes running to 1,200 pages or more. The costs so far exceeded the intake that the journal began to be a heavy financial burden and Cope was in frequent difficulties with his publishers. McCalla and Stavely published Vols. 12–19, later volumes were published by several different firms. As a result the NATURALIST often appeared irregularly and tardily.

But its editorial support and scientific value were maintained at a high level. Packard continued as editor until Volume 19, 1885, when he withdrew. He had been the principal editor for eighteen years. With Volume 20, 1886, J. S. Kingsley took Packard's place as co-editor with Cope and continued in that position until after Cope's death in 1897. At various times during Cope's management all the following persons were associate editors, usually for brief periods: E. A. Andrews, W. S. Bailey, C. E. Bessey, R. P. Bigelow, Elliott Coues, J. H. Comstock, W. H. Hobbs, F. C. Kenyon, F. S. Lee, H. C. Lewis, W. N. Lockington, H. C. Mercer, T. H. Morgan, O. T. Mason, W. A. Newbold, C. V. Riley, J. A. Ryder,

W. T. Sedgwick, Henry Seward, Erwin F. Smith, R. H. Ward, H. C. Warren, Clarence Weed, C. O. Whitman, G. H. Williams, Thomas Wilson, J. L. Wortman, Ellis Yarnell—twenty-eight in all, representing almost every branch of biology and geology. The wide interest in the NATURALIST could not be better shown than in this list of associate editors.

During the nineteen years that Cope owned the journal, 1878–1897, the entire list of his own publications included more than 900 papers[3]; of these 776 were published in THE AMERICAN NATURALIST, and 122 of them were editorials on many themes of current interest which appeared in a section called "The Editor's Table." Many of these editorials have present-day interest and deserve to be more widely known; all of them are interesting, many scintillate with wit, sarcasm, humor, for Cope had the habit of speaking "out of his liver and jaw." His last editorial was found on his desk after his death in April, 1897, and was printed in the NATURALIST for July of that year.

After the death of Cope, J. S. Kingsley continued as editor for three months and then R. P. Bigelow succeeded him. The August number for 1897 contained the following notice (pp. 699, 700): "CHANGE OF OWNERSHIP: THE AMERICAN NATURALIST has been purchased from the estate of E. D. Cope by a number of gentlemen who are interested in the advancement of the natural sciences. Dr. Robert Payne Bigelow, of the Massachusetts Institute of Technology, has accepted the post of editor in chief. He will be assisted by an Editorial Committee and by an able board of Associate Editors, whose names will be announced later." These associate editors were J. A. Allen, E. A. Andrews, W. S. Bailey, C. E. Beecher, D. H. Campbell, J. H. Comstock, W. M. Davis, D. S. Jordan, C. A. Kofoid, Chas. Palache, D. P. Penhallow, M. H.

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[3] See Henry Fairfield Osborn, "Cope, Master Naturalist." Princeton University Press, 1931.

Richards, W. E. Ritter, F. Russell, L. C. Russell, Erwin F. Smith, L. Stejneger, W. Trelease, S. Watase—truly a notable list of names.

The names of the gentlemen who purchased the journal from the Cope estate and of the editorial committee were not made public, but inquiry among some of the survivors indicates that one of the prime movers was the late Dr. W. McM. Woodworth, of the Museum of Comparative Zoology, and that C. B. Davenport and G. H. Parker were associated with him. R. P. Bigelow was editor beginning with the September number of 1897 and ending with the December issue of 1898. Thereafter no names of editors were published, but Dr. Bigelow remembers that Woodworth followed him as editor and that Parker took Woodworth's place when he was absent on expeditions with Alexander Agassiz. During this ten-year period from 1897 to 1907 the NATURALIST was kept alive and edited by this group of men at Harvard, the Massachusetts Institute and Tufts. It was published by Ginn and Company, Boston.

In 1907 J. McKeen Cattell acquired the NATURALIST and has continued to edit and publish it ever since, although his name did not appear as editor until 1925. Since 1939 Jaques Cattell has been associated with his father, and is now the responsible editor. In accordance with action taken at the annual meeting of the American Society of Naturalists held in Philadelphia on January 1, 1941, a committee drew up a plan for the organization of a board of consulting editors. The following have consented to serve in that capacity: W. C. Allee, University of Chicago; G. W. Beadle, Stanford University; L. J. Cole, University of Wisconsin; Th. Dobzhansky, Columbia University; C. L. Hubbs, University of Michigan; C. W. Metz, University of Pennsylvania; Karl Sax, Harvard University; A. Franklin Shull, University of Michigan, and L. J. Stadler, University of Missouri.

For more than fifty years the journal appeared as a monthly; in 1918 it was issued as a bi-monthly and has so continued. A study of its seventy-five volumes shows that it contains a great store of valuable material, much of which is overlooked because of the lack of a comprehensive index of the entire series. May this lack be remedied soon! As this oldest and best of American journals of natural history goes into the last quarter of its century, the American Society of Naturalists hails it with Rip Van Winkle's blessing: "May you live long and prosper!"

THE NATURALIST IN AMERICA[1]

DR. L. C. DUNN

SEVENTY-FIVE years ago there appeared the first number of a natural history journal which has since become the oldest American scientific periodical in its field. It was called *The American Naturalist—a popular illustrated magazine* and the names of its editors and of its contributors and the nature of its contents all indicate clearly what a "naturalist" was in those days. He was one who studied animals and plants. He might also be interested in minerals or weather or stars, but this interest was nearly always connected closely with animate nature. His method was primarily observation and description, in nature, for it was a time of exploration, of listing the animals and plants of the world, of study in the field, and there were few laboratories of zoology or botany in which any other method could be followed.

Many of those who published their observations in the NATURALIST had no academic connection. They were professional or business or literary men or men of leisure. As naturalists they were amateurs and the love they bore the study of natural history shines in many of the papers in that first volume. Both the contents and style of many of the papers in the early volumes show that those who wrote them were not pressed for time or hounded by ambition; they had the leisure to put their observations and questions into the polished literary form of the day. They owed their leisure, in part, to the commercial prosperity of the nineteenth century. Naturalists, in those days, often had incomes and could afford the leisure. In the same year when the NATURALIST began publication, young Alexander Agassiz met the young Professor Charles W. Eliot in the streets of Boston. He said:

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[1] Introductory remarks of the chairman of a symposium which the American Society of Naturalists had planned to hold at its meeting in New York in December, 1942. The symposium, which was to have had as subject "The Naturalist in America 1942 ± 75, Retrospect and Prospect," was intended to mark the seventy-fifth anniversary of the founding of THE AMERICAN NATURALIST. The meetings of the society were cancelled at the request of the Office of Defense Transportation. Two manuscripts intended for presentation at the symposium have been received and appear herewith. Others may appear in subsequent issues.

> Eliot, I am going to Michigan for some years as superintendent of the Calumet and Hecla Mines. I want to make money; it is impossible to be a productive naturalist in this country without money. I am going to get some money if I can and then I will be a naturalist. If I succeed, I can then get my own papers and drawings printed and help my father at the Museum.[2]

Agassiz made a lot of money and became a good naturalist.

In some of the papers sentimentality passed for love of nature and in only a few the purpose to be served was "science." The arts of observing, of recording, of cataloguing, of preparing specimens, of taxidermy, of adapting the new method of photography to the naturalist's needs stood before the science. It is the glory of the truly great naturalists that they make us forget the distinction between the art and the science, and a few of the early NATURALIST papers achieve this synthesis.

A shining example of the amateur naturalist stood before all in those days, one who by reason of inherited wealth could afford to be a naturalist and who by diligence and breadth of observation turned the art of the naturalist into a new foundation for all the biological sciences and created a new freedom for thought and speculation. "The Origin of Species" preceded the first volume of THE AMERICAN NATURALIST by only eight years; and Darwin's evidence as contained in "The Variation of Animals and Plants" appeared and was reviewed promptly in Volume 2. Darwin's views had certainly not prevailed in 1867, for the address of the president of the American Association for the Advancement of Science, Professor J. S. Newberry, was printed in Volume 1 of the NATURALIST and it contained these lines:

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[2] "Letters and Recollections of Alexander Agassiz," p. 61. Edited by G. R. Agassiz. London: Constable and Co. 1913.

> This much I have said in view of the possible acceptance of the Darwinian theory by the scientific world. I should have said, *in limine*, however, that the Darwinian hypothesis is not accepted and can never be fully accepted by the student of science who is inspired with the spirit of the age. From the nature of things it can be proved only to a certain point, and while we accept that which is proven,—and for it sincerely thank Mr. Darwin,—that which is hypothesis, or based only upon probabilities we reject, as belonging in the category of mere theories, to disprove or purify which the modern scientific reform was inaugurated.[3]

There were great naturalists in this great tradition then working in America and the new journal had to represent the interests of men like Agassiz, Cope, Coues, Dana, Hyatt, Leidy, Marsh, Packard and others of equal stature.

The activity of naturalists was coming into fruition in many ways in those days. The zoological museum at Harvard was new (begun 1859), the American Museum of Natural History was founded in 1869, and the summer settlement at Penikese Island, which gave rise to the Marine Biological Laboratory at Woods Hole, was founded by Louis Agassiz in 1873.

That was three quarters of a century ago. To-day THE AMERICAN NATURALIST still appears. Its nine consulting editors are all professional biologists from the universities, and seven of them represent fields of work which did not exist when the NATURALIST began, namely, genetics and cytology. In the issue for November–December, 1942, the eight papers all deal with genetical or cytological problems. The significant fact, however, is that all of them are concerned with the factors of evolution and this has been and continues to be the inquiry which unites and inspires naturalists. If these are "laboratory" papers (and all of them are) it only means that in 1942 the naturalist may work with the methods of 1942; and these must perforce be different from those of 1867. THE AMERICAN NATURALIST has become a professional journal. By no stretch of meaning could its 1867 masthead, "a popular illustrated magazine," describe its character to-day. The amateur naturalist has virtually no place in its pages, and art, by and large, has been replaced by science.

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[3] J. S. Newberry, THE AMERICAN NATURALIST, 1: 464, 1867. Annual address of the president, delivered at the meeting of the American Association for the Advancement of Science held at Burlington, Vermont, August, 1867.

The changes in THE AMERICAN NATURALIST illustrate what has been happening to biology generally in the United States. In these 75 years there have arisen many methods of study largely of a quantitative experimental nature which must be pursued principally in the laboratory. The goal of these studies appears to be analysis, rather than the synthesis which stood more immediately before the older naturalists.

These different methods of modern biology have led to apparent differences of purpose amongst the scientific descendants of those who called themselves naturalists. There are those whose interest clings to animals and plants as such, to the time-tested methods of observation in nature and to the older questions of evolution, phylogeny, selection, adaptation. There are others who, under the influence of physics and chemistry, hope to reduce the laws of living matter to the same terms of matter and energy which have proved themselves so universal in the other natural sciences. Some biologists of this persuasion tend to think that the day of the older naturalist is over; that the questions of the future will find their answers only as a result of radical experimental analysis. To this the upholders of the naturalist tradition retort (or seem to) that continued analysis, like hope deferred, sours upon itself, and, by gaining its satisfaction from minor facts, however exactly demonstrated, moves away from rather than towards the problems presented by animals and plants in nature. Since this apparent division among biologists has been recognized by so many, it has seemed to offer a good topic for discussion at this celebration.

This division may already be a thing of the past, for there are now many who study the old questions with the new tools, and for these there has always been and I suppose always will be a place in THE AMERICAN NATURALIST. They probably represent the naturalists of to-morrow.

On such an anniversary all students of nature may well ask themselves whether their purposes, their ideals and their hopes have changed; whether the new methods have brought new understanding of nature; whether they are content to pursue them in the new ways which are now themselves becoming old ways. There is a farther question which the readers and contributors to THE AMERICAN NATURALIST of 1942 must face. How will the naturalist tradition fare in the hard new world that is being born out of the war? These are questions with which the speakers in this symposium must wrestle.

While we gather to recall the fruitful history of this journal, we can take comfort for its future by contemplating its past. Its past has been good, partly because it has endured as a continuous thread connecting us with good naturalists of another day. We may wish it well for the next 75 years, seeing in the continuity of its purpose, apart from all the inevitable changes of its form and method, our best assurance of future good.

THE FUTURE OF THE NATURALIST[1]

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IF we choose to go by the lexicon, a naturalist is any student of natural sciences, no matter what technique he employs or how restricted the field of his specialty. In that sense of the word I am sure you will agree that the naturalist has quite a future, as well as a most respectable past.

If this were an ordinary tribunal, that should end the debate. We are, however, a group of natural scientists not content to accept written authority unless we can verify it from our own observations. And we have observed that many of our colleagues in the natural sciences do not consider themselves to be naturalists at all. This is certainly true of astronomers, physicists and chemists. It is increasingly true of geologists and biologists. So, regardless of the dictionary, something is happening to the word "naturalist." It becomes our business to find out what sort of change is going on, and to clarify the situation if we can.

So long as a language is alive, its words are malleable. The only exceptions are those words, *e.g.*, scientific terms, whose meaning is fixed by formal agreement. Yet every one of us who has worked behind the façade knows of instances where the tempering of a scientific term has involved more of rough-and-tumble than of either formality or agreement. I suspect this to be true of the term under consideration. It has an explicit definition of long standing, but we are not satisfied to use it in that sense. Its meaning has obviously been restricted. I am certain that in some quarters it has been degraded. Against this latter change I protest, and on that issue fix the debate.

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[1] This paper was prepared for the annual meeting of the American Society of Naturalists, which was scheduled to be held in New York City on December 29, 1942, but was cancelled owing to war conditions.

The classical division[1] of knowledge upon which our faculties have been constructed is four-fold. All recorded fact is history, its meaning is philosophy. All knowledge of man is moral, all else natural. By combination we have:

Moral history—the record of man.
Moral philosophy—the significance of this record.
Natural history—the record of nature, excepting man.
Natural philosophy—the interpretation of nature, excepting man.

In practice, while natural history concerned itself with observing the heavens, the earth and living organisms, natural philosophy was concerned with speculation about them. This speculation led to the mathematical analysis of astronomical observations, whereupon the astronomer ceased to regard himself as a natural historian. It led to chemical and physical experiment, whereupon the doctors concerned began to consider themselves natural philosophers. Natural history was left with only the botanists, zoologists and geologists on its hands, and to these practitioners the word "naturalist" was restricted.

As botany, zoology and geology have become increasingly technical and experimental in character, they too have dropped the rubric of natural history. Many of the scientists concerned seemed content, unless I am mistaken, to regard the term as obsolete or to use it as an *omnium gatherum* for any sort of superficial, uncoordinated study of nature that is out-of-doors and does not involve the use of apparatus. Also, if my observation is correct, the term "naturalist" has undergone, in the minds of many, a parallel change.

The distinction between a record and its meaning is still as valid as it ever was. History is one thing and philosophy another. But the course of science shows that the two can not, in practice, be divorced. The scientist, in seeking new facts, must be guided by the meanings already in his possession. He must, whatever his discipline, be at once natual historian and natural philosopher.

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[1] *Cf.* Sir David Prain, *Ann. Applied Biol.*, 8 (1): 66–76, 1921.

More than that, man can not always be considered apart from the rest of nature—probably not ever. The natural scientist can not avoid the fringes of moral history. As to moral philosophy, that is something no scientist can escape. The very decision to avoid it is a moral judgment.[2]

The elaborate specialization of knowledge may seem to have broken the four classical fields into fragments. This is an illusion. The efforts of specialists, consciously or otherwise, have instead blended them into a unity and broken down the once distinct walls between them. In this flux, what remains *of* the naturalist and what remains *for* him? To get at this problem I propose to consider an authentic, confessed and conceded, naturalist, Charles Darwin. Does he represent something once useful and vital, but now on its way out, like the ivory-billed woodpecker? After all, that is a fair question, for he himself remarked, "We need not marvel at extinction."[3]

The greater part of Darwin's working life was unquestionably devoted to natural history. He called himself a naturalist, and so he was. He observed living plants and animals and their environment. He observed, too, the records of the past. This did not prevent him from reflecting upon what he had seen—from behaving like a natural philosopher. Nor did it prevent him, when he saw good reason, from undertaking experiments. Some of these periods of experimental work were prolonged and the experiments were elaborate.[4] I am not aware that he considered himself the less a naturalist for that reason, although again he was behaving as a natural philosopher rather than a historian. A physiologist does not cease to be what he is when he steps out-of-doors to see if his experimental results on nutrition or sensory responses can be applied to situations occurring under field conditions. He remains a physiologist. The laboratory door does not lock behind him and bar his return any more than it swung shut to imprison Darwin and forever cancel his status as a naturalist.

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[2] An old saying, variously attributed, runs "Every man is a philosopher. For if you say, 'I am not a philosopher,' that is a philosophic judgment." In commenting on this A. Meiklejohn (personal communication) writes: "If I were making the assertion now I'd say, 'The man who denies he is a philosopher is one if he knows what he is saying, because, to know it, he must know what philosophy is; and if one knows that, one is a philosopher.' You see I leave out the people who neither affirm or deny it. Some people seem to come fairly close to absence of activity on the subject."

[3] C. Darwin, "The Origin of Species." Sixth edition. New York, 1883. P. 297.

[4] *Cf.* C. Darwin, "The Power of Movement in Plants." New York, 1881.

The distinctive thing about the work of Darwin, the naturalist, is not to be found wholly in his technique of observation and record. More deeply, it lay in his direction of approach to the unknown. He came at it, not from a single point of structure of behavior, but from the integrated picture of living nature. Of necessity he dealt with massive groups of complicated factors. Some of them he resolved. Others have been brilliantly analyzed by more modern workers. Some remain a challenge to our skill and cerebration. It would be a harsh judgment that called him superficial because he neither began at the small end nor awaited all the answers in detail.

There are parallel situations in other fields of science. No one would call builders of organic chemistry superficial because they were obliged to proceed with their work in the absence of a proper electron chemistry. Indeed they had to go ahead without being able to rationalize organic with the simpler inorganic chemistry. In mathematics the very power and beauty of the higher methods lie in their ability to "get behind what is behind" and deal with massives in advance of detailed analysis and computation. This is not to question that modern genetics, for example, has been necessary to illuminate, even to modify, the ideas of Darwin on variation. In a sense the detailed and critical work of the laboratory must always be a court of last resort. But that it is a sufficient source of scientific truth or the source of a higher kind of truth may at least be questioned. The great relationships remain in living nature, facts as uncompromising in themselves as the swing of a galvanometer or the splitting of a chromosome.

It was clear from Darwin's work that there had to be a science of heredity and variation. This indeed he predicted[5] and labored in his later years to develop, handicapped by his apparent ignorance of an obscure pamphlet from Bohemia. Later it seemed perfectly fitting for a group which called itself the American Society of Naturalists to devote its powerful sponsorship and many of its finest programs to the infant science of genetics. And the naturalists hung on, and kept their name and their sponsorship long after this science became one of the most intricate, precise and abstruse fields of experimental work. They saw it through, whether they all saw through it or not. I, for one, lost the thread some years ago, to my profound regret.

Certainly the idea of continuous descent and variation was near the heart of Darwin's work. But beneath it lay another idea even more fundamental—the inseparability of life and environment. Actually this idea was implicit in the first studies on material interchange and metabolism which began with the study of oxygen more than seventy years before "The Origin of Species" appeared. Darwin gave to it a proper emphasis and universality in the study of living organisms. Thereafter it became inconceivable to contemplate life divorced from the environment except as a matter of temporary convenience within the laboratory. It became inevitable, and should have been obvious, that there had to be a scientific discipline which approached biology as a problem of interrelationship of organism and environment. Darwin's own studies were a shining example of such an approach. The parentage of this new science was as august as that of genetics—indeed it was the same. But while the latter infant was publicly acclaimed, the former was slipped into the temple of learning through a side door and mumblingly christened "oecology."

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[5] C. Darwin, "The Origin of Species." Sixth edition. New York, 1883. P. 426. "A grand and almost untrodden field of inquiry will be opened, on the causes and laws of variation, etc."

Intrinsically, and from the standpoint of euphony, there should be nothing wrong with this term. Yet I marvel at its capacity to draw blank looks from the average layman, to say nothing of an occasional black look from the ordained. I saw a dean, himself a scientist, amazed at the erudition of a new college president who used the word familiarly in conversation. The dean afterwards (for he was a bluntly honest fellow) confessed that he did not know there was such a subject as ecology. Enlightened publicists, including H. G. Wells, Patrick Geddes, Lewis Mumford and Henry Wallace, have tried to get the word into familiar usage. Yet, not long ago, a discussion among congressmen boiled down to the question, "What [the hell] is ecology?"

For a time only two universities, both of them young and brash, gave the subject house-room in the United States. As recently as 1917, the biologists interested in this approach to their subject got such scant consideration from their parent societies that they had to organize their own. A number of the great universities still ignore ecology or accord it the bar sinister and tolerate it. One distinguished man, now dead, who was head of a great department, is on record as having written that he wanted a new man and it made no difference what his special interest was except that he did not propose to have an ecologist around.

I have made some effort to discover the retarding factor. There are of course crowded curricula, vested interest (which is another name for economic fear), preoccupation with other interests and on occasion, personalities which operate adversely against any new subject. These I pass by. More serious are two opinions: one, that ecology has no intellectual content or *raison d'être,* and is but the superficial emphasis of what every man knows; two, that it is the capsheaf of biological work and no one has any business meddling with it so long as we are so ignorant of many details which must be attended to first. While these are extremes of opinion, so long as they can be urged in good faith, they must be met.

Perhaps the readiest brief answer to them is to be found in the fruitful applications of ecological knowledge to urgent problems of land use and management by such men as Phillips, Weaver, Tansley and many others, and by the Soil Conservation and Forest Services. Rather than dwell upon these, however, I wish to examine the structure of ecological thought to see where its own professors may have been at fault.

In most presentations of ecology one looks in vain for such names as Lavoisier, Ostwald, Sumner, Kropotkin and Henderson. Darwin is usually mentioned in connection with his work on pollination and competition, if at all. His equally important work on mutual aid, so unfortunately overlooked by Huxley, is often disregarded. Yet these men I have named are among those who are largely responsible for the only body of theory which, as I see it, can impart a fundamental unity to the tremendous bulk of ecological data which is being accumulated.

Briefly, Lavoisier demonstrated the orderly character of material interchange between organism and environment. With the development of thermodynamics the relation of this to energy was clarified. Ostwald stated explicitly that all life and living communities were part of the cycle of solar energy, elaborations of available free energy. Henderson studied the environment, analyzing it in terms of material and the energy cycle and showing its ultimately controlling character. From the physical or environmental side these men established what Darwin had proved from the biological side—that life and environment had to be considered together. Sumner I have mentioned because of his theory of folkways, since brilliantly elaborated into the concept of human culture forms. It is these forms which, emerging from human behavior patterns, largely determine human relations to the environment.

More recently other workers have invited attention to the fact that the interrelationships with which ecology deals involve systems of dynamic processes whose effects are genetic. These systems appear to exemplify principles of equilibrium which are universal. The problems of ecology have extension and continuity in time as well as space.

It is not my wish, in thus indicating a structure of basic theory, to detract one iota from the importance of the conventional lineage of ecological thought. Humboldt, Schouw, DeCandolle, Haeckel, Warming, Schimper and their successors shine as brilliantly as before. Indeed their work becomes more luminous as we insist that it deals with organized elaborations of the energy and material cycle.

Nor do I wish to imply that ecologists do not increasingly understand this fact. I am talking about what gets into their teaching and their apologetics. As a matter of fact, Adams[6] has sketched an outline of fundamental ecological theory. Transeau has successfully developed the idea of an energy budget for the landscape in his "Textbook of Botany" (1940). In related fields the soils students Jenny and Nikiforoff,[7] whose viewpoint is essentially ecological, have a clear conception of biological energetics. The posthumous paper of Raymond L. Lindeman in the October, 1942, issue of *Ecology*, in which the nutrient dynamics of aquatic habitats are developed, is a further case in point.

To my mind such considerations dispose of any charge that ecology is either amorphous or superficial. It should be neither. It should be, like the higher phases of mathematics, a viewpoint and an instrument which enables us to get behind what is behind, to determine the larger relationships in nature and guide the resolutions of their factors by whatever analysis may be necessary.

In the early phases of any science, men must grope their way. This is not a tidy business, particularly by comparison with subjects secure in a long tradition of disciplined and critical procedure. It must be admitted, too, that all ecologists have not dealt with important problems, nor held themselves to the standards of rigor which were possible.

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[6] C. C. Adams, *Ecology*, 16: 316–335, 1935.

[7] *Cf.* C. C. Nikiforoff, *Sci. Monthly*, 52: 5, 422–429, 1941.

In this connection, the literature dealing with the North American grasslands is instructive. It can be fairly described as a century of guessing, more or less shrewd, by men who were often highly competent in fields other than ecology. In the end—and in a surprisingly brief time—the fundamental rôle of available moisture was *demonstrated* by *ecologists*.

Not everyone who sayeth Lord, Lord, hath known the Name. There are still courses in "ecology" which resemble the regurgitations of a none-too-powerful vacuum sweeper. Yet it is fair to say that editorial boards of ecologists are as exacting today as they need be.

I am indebted to Professor Dunn for the reminder that biology often attracts individuals who from temperament or experience avoid the quantitative problems of science. As he puts it, "at the opposite end of the spectrum from the mathematical, physical and chemical (practicioners) of biology are the naturalists—taxonomists, ecologists, morphologists, etc." This is true. The impulse to do scientific work is itself an artistic, intuitive thing. The feeling for the significance of form is strong in some men, just as others are preoccupied with quantity.

That either viewpoint has any intrinsic virtue above the other may be doubted. In science, at least, each has to be judged by its fitness to the end in view. Ecology has today reached the point where increasing use is being made of the quantitative procedures. But the important consideration seems to me to be that the good scientist will follow his trail and develop his methods as he needs them. In my opinion the avoidance of quantitative work, if deliberate, is more often due to mental hazard than to actual incapacity.

The late William Bateson would not be accused of any lack of appreciation for quantitative work. Yet he told me that he had been given up as a bad job by his mathematics instructors, and was handicapped all of his life by his ineptitude in that field. He returned the compliment done him by his teachers by saying that, if the subject had been presented by them as it is by their successors at Cambridge today, it would have aroused his highest enthusiasm. That he could have mastered it, no one familiar with his energy and penetrating intelligence can doubt.

I can not admit the argument that we have no business working at relationships in the natural environment until we know all there is to know about the anatomy, physiology and taxonomy of every organism that lives, and all there is to know about atmosphere and soil. I can not admit that the influence upon a community of lessened moisture supply is any less fundamental a fact than the physics of absorption or that the discovery of mutual aid within a species is a lower order of knowledge than the discovery of the neuromuscular behavior back of it. We need both kinds of knowledge and the mutual perspective they can supply.

What has all this to do with my topic? I have said that technically every student of the natural sciences is a naturalist, but that more and more of them reject the title. I have tried to show that Darwin considered himself a naturalist, and that the essence of his approach was the study of living organisms in their natural environment. I have tried to show that this approach is still a valid scientific procedure, which, under the designation of ecology, has a content and a possibility of organization that is intellectually respectable.

I should like to add that we are in the midst of a war of unprecedented tragedy and proportion and that this war is of itself a symptom of ecological maladjustment. I venture the opinion that until mankind looks upon its differences as arising from faulty adjustment within and among the communities of men and between those communities and their natural environment, there will be no peace in any real sense. For peace is not the breathing space between wars. It is the orderly adjustment of men to the world they live in, containing in its structure the implicit guarantee of continued order. This I submit is fundamentally an ecological problem. In saying this, I do not minimize what may be termed the spiritual aspects involved, for they must work themselves out in material relationships.

The ecologist, more than any other worker in biology, continues the tradition of the naturalist as exemplified by Charles Darwin. Whether he is content to accept the designation of naturalist is not important. A definition is, after all, merely an invitation to accept a term in a certain, defined sense. I should like to invite him, since the term is already in practice restricted from its classical meaning, to consider himself a naturalist. No one can compel him to do so.

But I should further like to invite the American Society of Naturalists to extend to him, whatever he may choose to call himself, the same encouragement and active assistance which has, in the past four decades, wrought such magic within the "grand and almost untrodden field of inquiry . . . on . . . variation."

CHONDRODYSTROPHY IN RHODE ISLAND REDS[1]

DR. F. A. HAYS

DURING the hatching season of 1943 from March 7 to April 11 a type of chick abnormality appeared exclusively in the offspring from one mating pen. This was an inbred mating consisting of a cockerel mated to two of his full sisters and eight of his half sisters. This was the first inbred mating in this line of birds and previous to this generation care had been taken to avoid related matings.

Seven of the ten females, including the two full sisters, produced chicks with the abnormality, the total being 172 normal to 54 abnormal. If both parents were heterozygous for a single recessive gene producing the character the expectation would be 169.5 normal to 56.5 abnormal. This was a remarkably close fit to a 3 to 1 ratio and no single family deviated further than 2½ to 1 or 4 to 1 from expectation.

This abnormality behaved as a lethal when present in homozygous condition and had a lethal effect even in the heterozygous individuals, as will be shown later.

Table 1 presents the complete hatching record of this pen. It will be noted that a considerable number of the embryonic deaths from the seven hens at 18 days were probably produced by the abnormality. When the eggs of these hens were taken from the incubator on the 22nd day 14 embryos were normal and 28 showed the abnormality.

Of the chicks that actually hatched from these seven hens, 140 were normal and 16 had the abnormality. An attempt was made to raise 12 of these abnormal chicks, but none survived longer than 7 days. The abnormal chicks could only crawl about on their abdomen and they were unable to open their beaks properly to take food and drink. With hand feeding on milk the largest survival period was 7 days.

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[1] Contribution No. 498 from the Massachusetts Agricultural Experiment Station.

TABLE 1

HIGH MORTALITY LINE—HATCHING DATES MARCH 7 TO APRIL 11

Eggs Set											
				Died about 18th day		Alive or dead in shell at full term		Hatched		Totals	
Bird	Total	Fert.	Dead before 5 days	Normal	Short	Normal	Short	Normal	Short	Normal	Short
W 160	35	33	9	6	3	2	3	9	1	17	7
W 184	38	35	1	5	0	1	0	28	0	34	0
W 228*	36	33	2	0	4	2	4	21	0	23	8
W 229*	35	33	0	4	0	3	7	18	1	25	8
W 753	39	37	0	2	1	2	3	26	3	30	7
W 1332	34	31	0	2	1	0	3	23	2	25	6
W 1334	39	37	3	4	0	4	0	26	0	34	0
W 1838	37	37	2	1	1	2	2	23	6	26	9
W 1839	34	30	3	3	0	1	0	23	0	27	0
W 1873	37	35	0	3	0	3	6	20	3	26	9
								From 7 hens			
								Obtained		172	54
								Expected		169.5	56.5

* Full brother-sister mating.

EMBRYONIC AND POST-EMBRYONIC MORTALITY

The mortality records of the chicks from the seven hens in which the abnormality appeared may be compared with the mortality record of the chicks from the three hens where chicks did not show the abnormality. These data are presented in Table 2.

Embryonic mortality was obtained by dividing the number of fertile eggs into the total number of dead embryos at the end of the incubation period. Live chicks

TABLE 2

EMBRYONIC AND POST-EMBRYONIC MORTALITY IN CHICKS

Lethal hens	Embryonic mortality to hatching Per cent.	Mortality from hatching to 6 months Per cent.
W 160	63.6	55.5
W 228	33.3	61.1
W 229	30.3	50.0
W 753	10.8	65.4
W 1332	16.1	62.5
W 1838	13.5	56.0
W 1873	31.4	40.9
Mean	28.4	55.9
Control hens		
W 184	17.1	39.3
W 1334	18.9	23.1
W 1839	23.3	47.8
Mean	19.8	36.7

that failed to emerge were not included in the calculations. The mean embryonic mortality for the lethal group was 28.4 per cent. compared with 19.8 per cent. for the control group.

Post-embryonic mortality in chicks was calculated for the first six months of life. This calculation was made by dividing the number of chicks banded, which includes only 8 of the 16 abnormal chicks, into the number dying in a six-month period. The mean mortality in the lethal group was 55.9 per cent. compared with 36.7 per cent. in the control group.

These data indicate that chick mortality was significantly greater for the mothers that carried the abnormality gene than for those lacking the gene. This applies both in the embryonic and post-embryonic stages.

CHARACTER OF THE ABNORMALITY

This abnormality was observed for the first time in 1943 in a line of Rhode Island Reds being bred for high mortality in a cooperative project with the Regional Poultry Research Laboratory of East Lansing, Michigan. To produce this generation one cockerel was mated to two of his full sisters and to eight of his half-sisters. Previous to this time related matings had been avoided. All parents appeared to be physically normal.

The morphological characters exhibited by the chicks having the abnormality were very uniform. The head was wide and flat with both mandibles greatly shortened to produce very blunt beaks which did not open readily to take food or water. The shape of the beak was normal, except for its extreme shortness. Upper and lower beaks appeared to meet normally and no evidence of the so-called "parrot beak" was observed.

Long bones of both the upper and lower limbs appeared to be much shortened with some thickening in the humerus and ulna and extreme thickening in the tarsometatarsus. The femur was very crumbly and lacked a complete and distinct periosteum. All leg bones were straight. There

TABLE 3
LENGTH OF LONG BONES IN CENTIMETERS

	Normal (Landauer)	Abnormal (Mass.)
Femur	1.85	1.40
Tibia	2.61	1.85
Tarsometatarsus	1.99	1.15
Humerus	1.36	1.25
Ulna	1.28	.90

was no evidence of curvature in the tibia or of abnormal position of the lower limbs. The legs were so short that the hatched chicks were forced to struggle about on their abdomen and they moved around very little. In weight the chicks were normal but there was evidence of large yolk sacs as shown by distended abdomens.

In Table 3 are presented measurements taken on some of our abnormal chicks together with the normal reported by Landauer (1941).

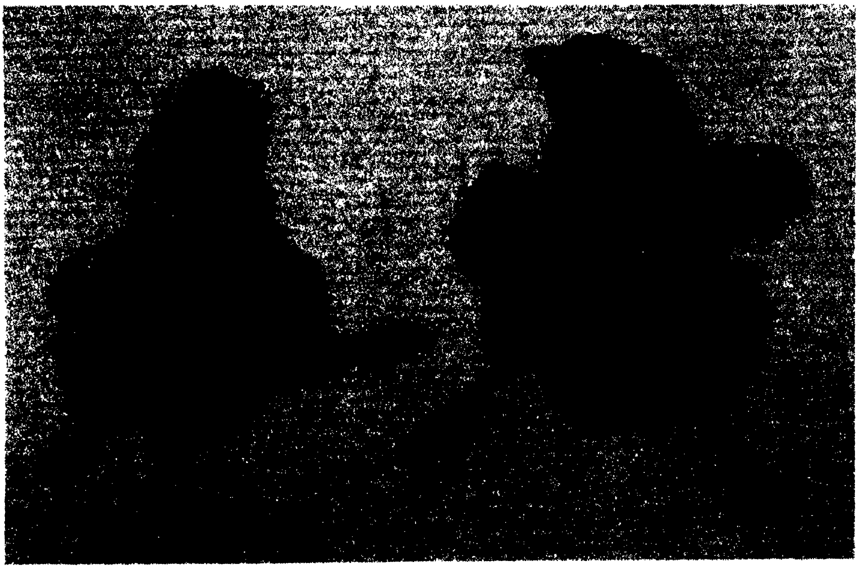

FIG. 1. Normal and abnormal chicks at hatching.—Mass Agr. Exp. Station.

DISCUSSION

The abnormality reported here does not appear to be the same as that reported first by Dunn (1923, 1927) and studied later by Landauer and Dunn (1926), Hutt (1929), Munro (1932), Upp (1934), Landauer (1936), Lyons and Insko (1937), Lamoreaux (1942) and Asmundson (1942).

The abnormality described here has several distinctive features.

(1) It is characterized by great uniformity in its effects.

(2) Many of the homozygous chicks hatch normally.

(3) It greatly shortens the long bones of both upper and lower limbs but the bones are straight.

(4) The beak is very short but the upper and lower members are properly proportioned.

(5) Size of chick is not greatly reduced.

(6) Carrier parents give an extremely close approach to a three to one ratio.

From the effects produced on the embryos and chicks, it seems probable that the condition is due to faulty calcium metabolism and this may justify the use of the term chondrodystrophy. Further study is being given to this abnormality.

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A POSSIBLE FUNCTION OF VITAMIN K IN PLANTS

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I. INTRODUCTION

THE importance of vitamin K in the clinical treatment of unnatural bleeding has encouraged physiologists and biochemists to engage in numerous studies of the effects of this vitamin on the physiology of animals. Already, an extensive bibliography has developed (Merck, 1940, 1941a, 1941b, 1941c). Even a list of reviews of the literature is impressive.

Vitamin K is widely distributed in plants. Dam and Glavind (1938) found that green tissues contained the highest concentration. Grasses and alfalfa leaves were reported by Cravens, Randle, Elvehjem and Halpin (1941) to be particuarly rich sources.

Despite the enormous literature describing the function of vitamin K in animals, there has been no attempt to define its significance in plants. Students have been so involved in the study of the vitamin requirements of animals that many have come to believe, at least by inference, that the chief function of vitamins in plants is to prevent vitamin deficiency diseases in animals and that the study of vitamin physiology is synonymous with deficiency diseases in animals. If we are to discover the fundamental activities of vitamins, we must study their reactions in the cells which produce them or require them. In other words, the "*cellular*" physiology of the vitamins, in plants as well as in animals, should be regarded as at least equally as important as their deficiency symptoms in animals, even though it may be many years before these studies can be completely related to each other.

The progress of the study of cellular physiology has been greatly aided by the many similarities between the behavior of animal and plant cells. In fact, it is cause for constant wonder, how closely the physiologies of plant and animal cells resemble each other. For example, the reaction of enzymes, the utilization of oxygen and the transfer of hydrogen in the respiratory processes are identical or nearly so. Many examples could be listed, but it is necessary only to remind the reader that these similarities exist. The purpose of the present paper is to present a theoretical basis for a possible function of vitamin K in plant cells. The argument is based on certain analogies with blood clotting in animals, the formation of limiting protoplasmic membranes in both plants and animals, and vacuolization in plants. A brief discussion of these phenomena is necessary to indicate their bearing on the problem.

II. DISCUSSION

Blood clotting: Although the process of blood clotting is not yet understood in all its details, the following three stages are generally recognized. In the first, the prothrombin-heparin complex reacts with the cephalin freed by the disintegrating platelets to form prothrombin and cephalo-heparin. In the second, prothrombin forms thrombin by a reaction which involves free calcium ions. Ferguson (1938) has described the quantitative relation of calcium and cephalin to this reaction. The third reaction occurs between thrombin and fibrinogen to form fibrin. Calcium is not required for this reaction. The total process may be summarized as follows:

(1) (Prothrombin-heparin) + cephalin → prothrombin + (cephalo-heparin)
(2) Prothrombin + Ca → thrombin
(3) Thrombin + fibrinogen → fibrin

Serum which exudes from freshly clotted blood causes clotting of fresh blood in the absence of calcium ions by virtue of the thrombin which it contains.

Precipitation membranes: Protoplasm is frequently described as a colloidal system dispersed in an aqueous medium but yet immiscible with water. This immiscibility is generally held to depend on a morphologically distinct membrane. Many prominent authorities have stated that ruptured protoplasm has the power to form a new membrane over the freshly exposed surfaces. The first significant observations were reported by Naegeli (1855), who observed the phenomenon in cytoplasm squeezed from the cells of *Chara,* grape and other fruits. De Bary (1859) described a similar phenomenon in the naked cells of slime molds. Strasburger (1876) studied *Vaucheria sessils;* Klein (1872) *Pilobolus;* Van Tieghem (1875) the Mucorineae; Pfeffer the root hairs of *Hydrocharis* (1877) and slime molds (1890); Sachs (1882) and Prowazek *Vaucheria;* Stübel (1908) *Nitella;* Seifriz (1921) *Rhiopus, Fucus* eggs and *Iris* pollen tubes; Nichols (1922) *Vaucheria, Cladophora, Chara* and *Nitella;* and Lepeschkin (1926) *Bryopsis.* The eggs of many invertebrates also formed a similar membrane when ruptured. Heilbrunn (1928) reviews the data from the eggs of *Stentor, Arbacia* and *Echinarachnius.*

So many respected authors have described the ability of ruptured protoplasm to maintain its morphological identity in water that some writers assume that this is one of its fundamental properties. Yet Dujardin (1838) early in the nineteenth century had observed that not all protoplasm behaved in this way. The protozoans which he studied sometimes dissolved in water when the cells were crushed. At other times, he followed in the field of the microscope the visible formation of a surface membrane when the cells were ruptured. Evidently immiscibility with water is not an inherent quality of protoplasm, but depends on the variable ability of the protoplasm to form a membrane over the exposed surfaces.

Heilbrunn (1927, 1928) pointed out that the formation of the membrane was independent of adsorption phenomenon because adsorption could not occur until some kind of boundary had been established, because low temperatures which favor adsorption retarted membrane formation and because the membrane did not form in the absence of free calcium ions. Eggs of *Stentor, Arbacia* and *Echinarachnius* were unable to form a precipitation membrane unless calcium ions were present. Strontium could replace calcium, but magnesium could not. Eggs crushed in solutions of sodium or other positive ions were unable to form a protective membrane. Chambers and Reznikoff (1926) found that amoeba quickly repaired tears in their surface membrane if they were in a dilute solution of calcium chloride, but were unable to do so in solutions of sodium chloride. Extracts of broken egg masses permitted surface precipitation by ruptured protoplasm in the absence of calcium. The presence of pigment granules also was found to be essential.

The stages in the formation of the precipitation membrane of invertebrate eggs were postulated by Heilbrunn (1928) as follows:

(1) Ca + pigment granules → ovothrombin
(2) Ovothrombin + protein → membrane

Since the ovothrombin of invertebrate eggs corresponds to the thrombin of the blood, Heilbrunn suggested that the term "cytothrombin" be used when the general reaction is considered.

The generality of this phenomenon for plant as well as for animal protoplasm is evidenced by the fact that Heilbrunn (1928) also found that extracts from crushed plant cells could hasten the coagulation of blood, presumably because the cytothrombin formed by the reaction of calcium ions with a protein during the crushing process could function as thrombin.

Vacuolization: According to Heilbrunn (1928) the formation of the precipitation membrane is initiated by the appearance of free calcium ions in the protoplasm. Internal precipitation of the protoplasm is prevented by the adsorption of the calcium ions on cellular colloids. Heilbrunn (1928) believes that any factor which releases calcium from internal colloidal surfaces will lead to the formation of localized, internal precipitation membranes. When this occurs, osmotic activities of the membrane result in vacuole formation. While this theory offers an explanation of that type of vacuolization involved in the formation of many small vacuoles, its application to the formation of the single large vacuole typical of many plant cells is uncertain. It is particularly significant in this connection that the figures by Sachs (1882) of ruptured *Vaucheria* cells show the formation of small vacuoles in the exuded part. It is not clear, however, why these internal precipitation membranes should be spherical, or at least shaped in such a manner that vacuoles appear as a result of their osmotic activity.

Cytolysis of the eggs of invertebrates, certain other types of animal cells and of plant cells may result if the processes of vacuolization proceeds far enough to cause the bursting and general disintegration of the protoplasm.

This theory of vacuolization is supported by the fact that physical as well as chemical agents which release calcium from colloidal surfaces cause the production of vacuoles and, in extreme cases, cytolysis. The agents known to affect both plant and animal cells in this way are distilled water, strong acids, strong alkalis, extreme cold, heat, electric currents, fat solvents, radium, x-rays and mechanical injury. It is interesting to note that this theory also accounts for the high viscosities of protoplasm obtained by Seifriz (1936) by microdissection. Any procedure as violent as manipulation with needles almost certainly would lead to the formation of internal precipitation membranes with a great increase in the viscosity of the mass.

Analogies between plant and animal protoplasm: The free calcium ions in the blood are unable to cause the formation of thrombin from prothrombin until cephalin has first removed the heparin from the prothrombin-heparin complex. Cephalin also occurs in plants and Harrow (1940) describes the ability of preparations from soybeans, cotton seeds and yeast to replace the cephalin from the platelets during the clotting process. It is not certain that a cyto-prothrombin-heparin complex exists in plant protoplasm, but the presence of cephalin suggests that it might function in some preliminary reaction similar to that in blood clotting. Heilbrunn (1928), on the basis of the work of several authors, has described the close analogy between the processes of blood clotting in animals and membrane formation, vacuolization and certain types of cytolysis in plant and animal cells. These similarities may be summarized as follows:

(1) An early stage involves a reaction between free calcium ions and a protein (= prothrombin) to give cytothrombin (= thrombin, ovothrombin).

(2) This stage is furthered by factors which release calcium ions from colloidal surfaces.

(3) A later stage involves a reaction between cytothrombin and a protein (= fibrinogen, pigment granules) to give a precipitation membrane (= fibrin, cytoplasmic membrane, vacuole membrane).

(4) The necessity of the ionized calcium is eliminated by the presence of the extracts from cell masses containing cytothrombin (= fresh blood clots, crushed invertebrate eggs, crushed plant cells).

(5) Cytothrombin from plant and animal cells is more or less similar, since extracts of crushed plant cells hasten the clotting of blood.

III. FUNCTION OF VITAMIN K

It is now generally recognized that vitamin K is intimately concerned in the process of blood clotting. Elliott, Isaacs, and Ivy (1940) found that subcutaneous injection of this vitamin corrected the tendency to hemorrhage and shortened prothrombin time in rats. Cravens, Randle, Elvehjem and Halpin (1941) reported that the blood-clotting time of day-old chicks depended on the amount of vitamin K in the ration of the hen. A diet containing 2 per cent. dried alfalfa leaf or 1 per cent. of dried cereal grasses allowed an adequate intake of vitamin K by the hen. Schonheyder (1938) also reported the relationship between the plasma prothrombin and vitamin K for chickens. A diet free from vitamin K was shown by Stefanini (1940) to decrease the amount of prothrombin in rabbit blood. The use of vitamin K to shorten the clotting time of the blood of infants, by increasing the prothrombin has been described by Waddell (1939). Hogan and Johnson (1936) reported that vitamin K in extracts of alfalfa or of young cereal grasses in the diet of guinea pigs lessened the number of young to die from hemorrhage at birth. The general clinical importance of vitamin K has been studied by many workers, and a large number of reviews of the literature have been published.

The wide distribution of this vitamin in plant cells suggests some fundamental significance in the physiological processes of plant cells. So specific is the relationship of vitamin K to the prothrombin level in blood that it has been called the ''antihemorrhagic'' vitamin. The close similarity between the process of blood clotting and the phenomena of membrane formation and vacuolization in plants suggests that it is not improbable that vitamin K is concerned with the formation of a ''cyto-prothrombin'' in plant cells which is a necessary precursor to the formation of precipitation membranes and vacuoles.

IV. SUMMARY

The formation of precipitation membranes by plant protoplasm resembles the clotting of blood in the following respects: (1) In blood cephalin frees prothrombin from the prothrombin-heparin complex. Cephalin is found also in plant protoplasm where it may have a similar function. (2) Free calcium ions are necessary for the formation of a cytothrombin (= thrombin, ovothrombin) from a protoplasmic protein (= prothrombin). (3) Chemical and physical agents further this process by freeing calcium ions from colloidal surfaces within the protoplasm. (4) Cytothrombin reacts with a cellular protein (= fibrinogen, pigment granules) to give a precipitation membrane (= fibrin, cytoplasmic membrane, vacuole membrane). (5) The necessity of free calcium ions is eliminated by the presence of extracts of cell masses containing cytothrombin (= fresh blood clots, crushed invertebrate eggs, crushed plant cells). (6) Extracts of crushed plant cells hasten the clotting of blood.

The necessity for vitamin K in the formation of prothrombin in blood suggests that it may be concerned with the formation of a "cyto-prothrombin" in plant protoplasm. This substance could be a precursor of the precipitation membranes which prevent the dissolution of plant protoplasm in water and also to permit the formation of vacuoles.

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THE MAINTENANCE OF VITALITY IN PURE LINES OF THE CILIATE *TILLINA MAGNA*[1]

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THE most extensive study made to date on the structure and life history of *Tillina magna* is that of Gregory (1909), who placed the ciliate in the order Holotrichida, suborder Trichostomina, family Chiliferidae. Gregory found her specimens in a laboratory jar containing a horse-manure infusion and suggested that the organism possibly might be a facultative parasite of the horse intestine. However, it is now generally agreed that while Gregory's order and suborder designations are correct, *Tillina* is actually a member of the Colpodidae, as Kahl (1931) and Turner (1937) have pointed out. Furthermore, there is no satisfactory evidence that *Tillina magna* may occur as a facultative parasite of the horse. It is unmentioned in Hsiung's monograph (1930) on the intestinal protozoa of the horse, and the records of its occurrence, while not at all plentiful, show that it is to be regarded exclusively as a freshwater ciliate.

Gruber (1879) established the genus and species, and described the method of division within a thin-walled cyst. His specimens came from a small aquarium into which dried mud from Vienna had been put. Evidently the mud contained dried protective or resting cysts. Ilowaisky (1921) found *Tillina magna* in freshwater pools in the vicinity of Saratov, though he described it as *Pseudocolpoda cochlearis cienkowskii,* and Bresslau (1922) found it in infusions made from meadow turf. I have taken it repeatedly in the past five years from tem-

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[1] I am indebted to Dr. C. V. Taylor, professor of biology in Stanford University, for generously placing at my disposal the facilities of his laboratory during my tenure of a leave of absence on the Kenan Foundation of the University of North Carolina.

porary pools in a meadow near Chapel Hill, North Carolina. Following prolonged rains these pools yield active tillinas. In periods of summer drought when the pools disappear the bottom debris yields dried protective cysts which activate readily upon transfer to water. These specimens agree in all respects with Kahl's description (1931, p. 282) of *Tillina magna.*

Of the many observations made by Gregory on the general biology of *Tillina magna,* the following may be mentioned as having a special bearing on the present study. Reproduction occurs only by the formation of spherical division cysts, within which the parent organism undergoes usually 2 successive cell divisions. Upon the rupture of the thin cyst membrane the 4 offspring emerge as fully developed individuals, merely smaller than the parent. Under favorable conditions this process occurs once a day, and the 4 individuals so produced are counted as 2 generations. Thick-walled protective or resting cysts are also formed under certain conditions—chiefly adverse ones.

In her life history studies Gregory established 2 pure lines, each consisting of 4 sublines, which were maintained on horse-manure infusion in depression slides, since *Tillina* is a bacterial feeder. Both lines showed periodic fluctuations or rhythms in the reproductive rate, which Gregory considered to represent "periodic variations in the vitality of the protoplasm" and to be independent of environmental changes. As generations passed both lines showed a gradual decline in vitality which was expressed first in a progressive decrease in the rate of division and later in the death of the lines. The first line produced 210 generations in the 112 days of its life; the second, 548 generations in 405 days. Attempts to stimulate the declining lines by a variety of chemical and physical means were largely unavailing, and the conclusion was reached that in *Tillina* the passage of generations results in a gradual decrease in the vitality of the protoplasm. By what means, natural or artificial, this inherent tendency toward decline and death may be offset was not made clear by Gregory.

Reference may be made to Calkins (1933, pp. 244–260) for a discussion of the problem of vitality in ciliates and for a critical evaluation of the results of a considerable number of studies that bear upon the problem.

The present study was begun in an attempt to answer the following questions. Can an entirely satisfactory and wholly reproducible culture method be devised for *Tillina magna?* Does *Tillina* under adequate and constant conditions of culture show periodic fluctuations in the rate of reproduction and suffer as generations pass a decrease in vitality that terminates in death?

The success of Taylor and his associates (e.g., Taylor and Strickland, 1938) in culturing *Colpoda duodenaria* on a suspension of the bacterium *Pseudomonas fluorescens* in a buffered, non-nutrient solution of inorganic salts of Na, Mg, K and Ca suggested the use of a similar procedure in culturing *Tillina*. Accordingly, a solution having a total salt content of 0.012 per cent. was prepared with Pyrex-distilled water and its pH value was adjusted to 6.8, following the directions given by Barker and Taylor (1931, p. 622). To each 5 cc of this solution was added a heaping loop of *Pseudomonas fluorescens,* which was grown on Difco nutrient agar. Unfortunately, the use of this medium for the growth of *Tillina* was disappointing, in that the animals instead of spiraling smoothly or feeding leisurely on the bottom—characteristic features of their normal behavior—would swim rapidly in small circles just beneath the surface film and on occasion would burst and disintegrate. That there was nothing essentially toxic or injurious to ciliates in the medium was shown by the fact that both *Paramecium caudatum* and a species of *Colpoda* could be grown in it with complete success. Many different concentrations of the salt medium and many modifications of the formula were tested, but in none did *Tillina* react normally and grow satisfactorily. Hence, the use of a completely reproducible, non-nutrient medium with bacteria added was reluctantly abandoned, and out of expediency a culture medium made as follows was adopted. To 4 cc of the 0.012 per cent. salt medium of pH 6.8, one cc of 0.05 per cent. sterile lettuce infusion (prepared by boiling 0.1 gm powdered dried lettuce 5 minutes in 200 cc water) and the usual loop of bacteria were added. In this medium, which will be referred to merely as "lettuce medium," *Tillina* invariably reacted normally and flourished. I am unable to explain satisfactorily the lack of tolerance shown by *Tillina* for any of the inorganic solutions tested. The evidence indicates that *Tillina* lacks the capacity for adjustment to chemical and physical changes which certain other ciliates are known to possess, and this circumstance may account for the seeming rarity of *Tillina* in nature.

To obtain specimens for vitality studies resting cysts were transferred into fresh 0.05 per cent. lettuce infusion as a means of activation. These cysts were 7 weeks old and represented a wild population which had encysted in an old lettuce-infusion culture when the food supply became exhausted. Active individuals emerged from nearly all of the cysts after approximately 3 hours in the excysting infusion, and several of these were isolated in depression slides in lettuce medium. On the following day 2 pure lines (designated as A and B) each consisting of 4 sublines were established with the progeny of 2 of the excysted specimens. In this process each ciliate was isolated in 0.2 cc lettuce medium in a clean depression slide, and the slides were transferred immediately to moist chambers which were kept in a constant temperature oven at 21° C. The arrangement was such that the cultures received 8–12 hours of light each day, as they would in nature. On each succeeding day 4 of the progeny of each pure line were transferred to clean slides and fresh lettuce medium. Records were made daily of the number of divisions undergone by each subline in the preceding 24 hours, and from these the average daily fission rate per line (A or B) was calculated. Thus the animals were grown under conditions of as high a degree of constancy as their somewhat refractory nature permitted, though it is recognized that the addition of lettuce infusion to the medium introduced a potential variable, particularly with reference to the bacterial flora. However, it is believed that the daily changes to fresh lettuce medium, the use of consistently clean glassware and the briefest possible exposure of the cultures to room air at the time of transfer so restricted the growth of contaminating bacteria that their presence was without significance.

The 2 lines were cultured for a period of 220 days, whereupon the experiment was discontinued. In this period Line A produced a total of 579 generations, and Line B, which had consistently a slightly lower division rate, 525 generations. Since the cultural histories of the 2 lines were essentially identical, only that of Line A will be considered in detail.

In Table 1 the average daily fission rates of the 4 sublines of Line A are averaged further for 10-day periods (column 2), and the total number of generations through each successive 10-day period is calculated (column 3). Examination of column 2 shows that the rate of reproduction was remarkably constant throughout the experiment, varying only from a minimum production of 25 generations (an average of 2.5 fissions per day) in the 8th, 13th and 21st periods to a maximum of 28 generations (2.8 fissions daily) in the 19th period. Since the lines produced an average of 2.63 generations daily throughout their life, these departures from the average, amounting at most to only 6.5 per cent. in the case of a production of 2.8 fissions, can scarcely be considered to have significance. In view of this fact, it is evident that the division rate was as high at the end of 220 days or 579 generations of culture as it was when the lines were established, and there was no evidence of a decline in vitality as measured by the division rate. Furthermore, under the constant conditions of the experiment there was no indication of periodic fluctuations or rhythms in the reproductive rate.

It is well known that diminished vitality in ciliates may express itself not only in the division rate but in structural abnormalities and in a decrease in the size of the animals (Maupas, 1888). In the present study neither the active tillinas nor the division cysts showed any structural departures from the normal or any decrease in size as generations passed. Ten active specimens of maximum size selected at random from Line A in the first 10-day period measured on the average 268 μ × 183 μ, and 10 division cysts had an average diameter of 205 μ. The dimensions of active specimens and cysts from later periods showed no significant departures from these measurements. For example, 10 division cysts from the 11th period had an average diameter of 198 μ, and 10 from the 22nd period, a diameter of 207 μ. These measurements furnish additional evidence of sustained vitality throughout the experiment.

TABLE 1

SUMMARY OF RATE OF REPRODUCTION OF A PURE LINE OF *Tillina magna* UNDER CONSTANT AND ADEQUATE CONDITIONS OF CULTURE. NOTE THAT NO LOSS OF VITALITY AS MEASURED BY THE FISSION RATE OCCURRED, EVEN AFTER 579 GENERATIONS OF CULTURE.

Successive ten-day periods	Total average number generations for the period	Total average number generations to date
1	27.0	27.0
2	27.5	54.5
3	26.5	81.0
4	25.5	106.5
5	26.5	133.0
6	26.0	159.0
7	27.0	186.0
8	25.0	211.0
9	26.5	237.5
10	25.5	263.0
11	27.0	290.0
12	27.5	317.5
13	25.0	342.5
14	26.5	368.5
15	26.5	395.0
16	25.5	420.5
17	27.5	448.0
18	26.0	474.0
19	28.0	502.0
20	25.5	527.5
21	25.0	552.5
22	26.5	579.0

Endomixis was never observed in the active specimens of either line, nor did conjugation occur at any time among individuals of the lines or among their surplus progeny. Attempts to induce conjugation in small populations by increasing the temperature, varying the amount of the food, altering the pH and changing the salt content of the medium ended without exception in failure. As a matter of fact, conjugation has never been reported in *Tillina.*

Likewise, the spontaneous formation of protective cysts was never observed in the lines, though such cysts could be produced at any time by allowing the food supply to become exhausted. Unlike *Colpoda duodenaria* (Taylor and Strickland, 1938), washed tillinas could not be deprived of food and made to encyst reliably in any inorganic medium that was tried. Their behavior in such solutions, as has been stated, was never entirely normal and their fate was unpredictable. A tillina might burst soon after transfer or after many hours, it might swim continuously for 4 days and perish, or it might divide to form 2 offspring which might or might not encyst. On the contrary, surplus animals from the pure lines if left in lettuce medium could always be depended on to produce protective cysts after 2 or 3 days. That such cysts resulted from absence of food was readily demonstrated. If additional bacteria were put into the cultures at intervals over a period of several days, reproduction continued without the formation of resting cysts, until as many as 500 or 1000 active tillinas and division cysts were present in each of the small amounts (0.2 cc) of lettuce medium. Later these specimens formed protective cysts. Such cysts remained viable for 6 months or longer and never showed spontaneous activation, as do cysts of *Colpoda duodenaria* under certain conditions (Taylor and Strickland, 1938). The ability of the pure lines to produce normal resting cysts at any time is further evidence of sustained vitality in the lines, for Beers (1928) and Johnson and Evans (1939) in studies on *Didinium nasutum* and *Woodruffia metabolica,* respectively, have shown that impaired ability to produce resting cysts is an accompaniment of lowered vitality, induced, however, in their studies by dietary inadequacies and not by the passage of generations.

The evidence adduced from the present study shows that in *Tillina magna* there is nothing in the nature of a definite life cycle embracing a period of high vitality followed by progressively diminishing vitality and death as generations pass. The history of a pure line in the laboratory or of a population in nature appears to be purely a function of the environment. Under favorable and adequate conditions of culture, *Tillina magna,* like *Didinium nasutum* (Beers, 1929) and *Woodruffia metabolica* (Johnson and Evans, 1939) appears to be capable of indefinite reproduction without loss of vitality and without recourse to endomixis, conjugation or to the production of resting cysts.

The decline in vitality and the rhythms observed by Gregory were undoubtedly the results of the variable and inadequate conditions under which cultures were maintained in the earlier years of pure-line investigations—conditions which have since been vastly improved by the utilization of constant temperature apparatus and by the employment of pure strains of bacteria. The temperature varied greatly in Gregory's experiments, as she herself points out (pp. 401 and 403), and both the nature and the number of bacteria available as food were quite uncontrolled. It is well known that changes in temperature regularly produce fluctuations in the rate of reproduction of infusoria, and that any failure to control the quality and the quantity of the food available to animals under investigation, whether protozoan or metazoan, constitutes without exception a potential experimental variable. Whatever may have been the factors involved in the decline observed by Gregory, the fact remains that under the conditions of culture maintained in the present investigation the lines of *Tillina* failed to exhibit either rhythms or diminution in vitality.

SUMMARY

Two pure lines of the freshwater ciliate *Tillina magna* were maintained in lettuce medium on the bacterium *Pseudomonas fluorescens* for 220 days. In this time they produced a total of 579 and 525 generations, respectively. Under the constant conditions of culture employed, rhythms in the reproductive rate were absent. Neither conjugation nor encystment was observed, and the formation of protective cysts occurred only in subcultures when the food supply became exhausted. When the lines were discontinued, after 220 days, the vitality of the animals as measured by the fission rate was unimpaired by the passage of generations, and their size and structure were normal. The results indicate that in *Tillina magna* there is nothing in the nature of an intrinsic life cycle embracing in succession states of high vitality, decline and death.

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REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

IN this section reviews and notices are given of current publications on general biology and of specialized works which have an important bearing in this general field. Emphasis is given to books and major articles which fall within the special scope of THE AMERICAN NATURALIST, in that they deal with the factors of organic evolution.

REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

Man's Unknown Ancestors The Story of Prehistoric Man. By RAYMOND W. MURRAY. Milwaukee: Bruce Publishing Co., 1943: i–xiv, 1–384, 36 pls. $4.25.

THE STAGE for this semipopular recital of prehistory was set by swift-moving advances, during the pre-holocaust decade, in our knowledge of human evolution. The interlude of the war has permitted an appraisal of the great mass of new evidence, has made possible a collation of the diverse interpretations, and has allowed a book on the lineage of man to remain up-to-date during its printing. The non-specialist is given résumés of Weidenreich's epochal work in China and of von Koenigswald's in Java, on the evolving semi-humans generally known as *Sinanthropus* and *Pithecanthropus* and on the more truly human kinds which followed in those countries; of the enlightening new discoveries concerning different races of Neanderthal men; and of other researches on prehistoric men in Africa, Eurasia and the Americas. The author tentatively adopts but does not consistently follow Weidenreich's new synthetic classification of fossil men into three divisions: division 1, *Homo erectus,* with two subspecies—*H. e. javanensis* (preferably *H. e. erectus,* to accord with the International Rules of Zoological Nomenclature), which is a new alignment of *Pithecanthropus erectus,* and *H. e. pekinensis,* in place of *Sinanthropus pekinensis;* division 2, *Homo neanderthalensis,* with *soloensis* of Java and *rhodesiensis* of South Africa as subspecies; and division 3, *Homo sapiens*. The family tree of man is pictured as extensively branched, with a wide evolutionary range in existence at each time level.

Professor Murray's treatment strikes me as thorough, conservative and judicious. I arrive at this appraisal chiefly from his account of the discoveries of early man in America, particularly in the desert regions, since this is the only field of prehistory which I have made any attempt to follow. He states, but not dogmatically, that the evidence strongly confirms the views of certain workers that man lived in North America, in company with extinct mammals, during the early postglacial period, approximately 10,000 to 25,000 years ago, and may have existed on the continent during glacial and interglacial time.

To a limited degree throughout the book, and extensively in the final chapter, the author engages in discussions of "Prehistory and Religion." Much of this argumentation is essentially a defense of the Catholic position. The conflicts between prehistory and religion and between evolution and religion are pictured as discordances between science and Fundamental Protestantism. Catholic scholars are indicated as willing to allow or accept evolution, even of man's body and brain (but not of his soul) and as free to interpret the Biblical account of Genesis as figurative (but never as in substantial error, and never as in any way contrary to the limits defined in Rome). Such discussions will strike many readers as unpleasantly out of place, definitely anachronistic. However, the only interpretations in the book which seem flavored by religious views are the attempts made now and then to line up anthropological findings with the Biblical legends. Let us remember that the vision of many potential readers of "Man's Unknown Ancestors" is still blindfolded by religious myths. Professor Murray's book may open their view to the glorious horizon of science.

Man, Real and Ideal Observations and Reflections on Man's Nature, Development, and Destiny. By EDWIN GRANT CONKLIN. New York: Charles Scribner's Sons, 1943: i–xvii, 1–247. $2.50.

A DEEP-THINKING biologist gives in this readable little book a fine philosophy of human biology. He strikes a compromise—at times may seem to waver—between mechanism and vitalism, but since his mechanism is thoroughly grounded in rich biological experience and since his concepts of vitalism are very broad, his pen picture of life in general and of human life in particular is a very logical one. He reaches compromise more by addition than by averaging, for he accepts most of the fundamental facts and interpretations of mechanistic biology, but builds thereon a philosophy of creative synthesis. Similarly, instead of taking sides or trying to straddle the line between science and art, or between science and religion, or between science and ethics, or between the intellectual and the spiritual, or between the real man and the ideal man, he accepts both elements in each contrast.

The first part of the book, dealing with "The Human Species," contains much biological wisdom. For example, the author stresses the point that "individually acquired adaptations are fundamentally similar to normally inherited ones, and it is difficult to resist the conclusion that the two must be results of similar causes." The parallelisms between mutations and responses are also pointed out. The conviction is reached that "man is the last, best hope of future evolutionary progress in body, mind, and society." "The lesson of evolution is full of hope for the future, a real 'gospel' to a distracted world."

In the relatively extensive treatment of the "Development of the Individual" (Part II) the author brings out his summational philosophy of mechanism and creative synthesis: "Mechanism is universal, but so also is finalism . . . These two aspects of life are not antagonistic, but complementary."

The third part of the book, "The Real and the Ideal" starts with a very able and convincing defense of science, continues with a discussion of the role of science and of ethics and religion in human life, and ends with an essentially non-biological discussion of current problems of war, peace and international politics. The final conclusions, however, are that:

> The long course of organic evolution justifies faith in further progress . . . There has been no permanent retreat in the evolution of intellect, reason, and ethics. These are the perfecting principles in human life and evolution . . . We are today only children in the morning of time, and before us lie the countless centuries and millenia of man's vast future.

Genes and the Man. By Bentley Glass. New York: Bureau of Publications, Teachers College, Columbia University, 1943: i–xii, 1–386, figs. 1–108. $3.50.

"This Volume," the author tells us, "has been prepared to indicate a new outlook, not to present genetics or cytology, or embryology, or physiology, or even a summary of all of them, but rather to describe the operation and interaction of those factors which make the physical man, insofar as we know them or can reason about them today." "Throughout the realm of science," he wisely observes, "the narrow, rigid boundaries of specialized fields of subject matter are at last breaking down. The boundary between genetics and cytology has already disappeared, and it is now evident that embryology and physiology are beginning to enter the amalgam. As yet, however, the trend is apparent only in the more technical studies." Professor Glass has therefore essayed an elementary synthesis of the sciences which contribute to our understanding of the ontogeny of man. While realizing that his experiment in this direction has met with marked success, many will wonder why he left out of his "amalgam" all but the most incidental treatment of evolutionary biology (beyond the field of genetics). He attempts to answer, What makes man?, but fails to consider, What made man? Social evolution is also neglected, as in the final conclusion that our genes are all that survive us.

I will not attempt an appraisal of the pedagogical advantages or shortcomings of "Genes and the Man," beyond observing that there is evident no regular gradation from known to unknown or from simple to complex. The presentation throughout is a mosaic of the elementary and the technical. Perhaps this is as it should be.

The scope of treatment involves the danger of portraying man as an isolated phenomenon. This peril, however, is largely avoided by frequent comparisons of the structures and functions of other organisms with those of adult man, or with those of the corresponding stage in embryonic development.

The work is technically sound, the diction good and the diagrams clear-cut. The half-tones, however, are pepless. *C'est la guerre,* perhaps.

Naturalist at Large. By THOMAS BARBOUR. Boston: Little, Brown & Co., An American Monthly Press Book, 1943: i–xii, 1–314, 23 pls. $3.50.

BRIMFUL of grand personality, this literary treat gives us, in his own words, much as he would tell them during lunch in his famous Eateria or at smoke-time on the back stoop of M.C.Z., the life story of Thomas Barbour, fascinating incidents from his almost endless travels, keen appraisals of his acquaintances, and a little of his biological philosophy. Tom Barbour's heart grew out of proportion to the frame that holds it, and that, in the language of the street, "is something." He is not only an outstanding investigator, administrator and counselor, but also the kindliest and wisest *patrón* of naturalists and of natural history institutions. In some of his many effective acts he takes just pride, for instance in the development of Barro Colorado Laboratory in the Canal Zone and of the Harvard Garden at Soledad in Cuba, and in the bringing of new light, figuratively as well as literally, into America's greatest university museum. On other accomplishments he maintains a modest silence. A host of younger men to whom he has given a strong hand of fatherly help will do a lot of between-line reading. There are few, in the biological sphere, to whom "so many owe so much"; and, we suspect, there are few who have gained more full-hearted satisfaction out of doing so much for so many.

Here and there throughout the book and particularly in the appended "For Zoographers Only," Dr. Barbour gives us some of the conclusions which he has reached as results of his rich experience in the field of zoogeography. He is an advocate of the land-bridge origin of the faunas and floras of the West Indian and East Indian islands.

In "The Tests of Evolution" he stresses the unknown and possibly unknowable why's of organic evolution. For him there remains much room for religious faith. With approval he quotes Regan in circumscribing the role of mutation in speciation, and Cope in postulating a " 'super-abundant growth force'—growth in a particular direction until it becomes fatal." Some of us who have had the privilege of knowing Dr. Barbour personally (and know him now much better after the reading of his grand book), would like to take friendly issue with him in person on some of these points—or to talk with him on any subject of his own choice; he is always interesting and inspiring.

Physiological Regulations. By EDWARD F. ADOLPH. Lancaster, Pa.: The Jaques Cattell Press, 1943: i–xvi, 1–502, figs. 1–186. $7.50.

I OPENED this book with the expectation of finding therein a detailed contribution on progressive evolution, for I had recently been deeply impressed by Julian Huxley's view that greater independence of the environment, along with greater control over the environment, is a main criterion of biological progress. In this respect I was abruptly disappointed. Adolph shies from any considerations other than those of quantitative data which may be tabulated or graphed. He tells us:

> Like other students of biology, I was repeatedly told that regulations were important. What they were and how they operated was far from apparent.

> Gradually they acquired meaning, not as inferences from metaphysics, but as hazy inductions from biological experience. More recently I observed data concerning balances, variabilities, recoveries, and behaviors that manifest a common bearing upon the maintenance of properties. Bit by bit I have come to realize that this pattern of maintenance is probably what my preceptors were talking about. But, as a result of my backwardness I have an unforeseen advantage over them, for I build my abstractions about equilibration diagrams and frequency diagrams, while they used words. My concept is in quantitative and dimensional form, theirs was, I infer, less definitely founded.

Despite its size this volume is not a general treatise on physiological regulations. It is essentially a report on the author's extensive experiments. Though the discussion of regulations in the water relations of animals occupies about 300 pages, there is no adequate phylogenetic analysis of water-regulating mechanisms; hardly a mention, even, of the extended researches of Homer Smith, E. K. Marshall and others on the very interesting methods by which different groups of fishes control the amount of water in their systems.

I take it that "Physiological Regulations" is a tremendously important addition to the literature of physiology, but its contribution to evolutionary thought is limited to the extensive data which may be utilized by others, less adverse to philosophical interpretation.

Studies in the Life History of the Song Sparrow II The Behavior of the Song Sparrow and Other Passerines. By MARGARET MORSE NICE. Trans. Linn. Soc. N. Y., 4, 1943: i–viii, 1–328, 1 pl., figs. 1–6. $2.00.

WITH the publication of Part II of her 15-year study Mrs. Nice has made the Song Sparrow (*Melospiza melodia*) of the northeastern United States perhaps the most thoroughly known wild bird in the world. Part I dealt with matters of vital statistics—population and reproduction; Part II treats the behavior of the Song Sparrow and other passerines. It is, in fact, practically a monograph on bird behavior (about 420 species of birds are referred to).

Mrs. Nice's study is a splendid example of a comprehensive, well-planned campaign of field investigation carried through a number of consecutive seasons, then thoroughly correlated with the world scientific literature and carefully prepared for publication in the most usable form. Each chapter is well organized and fully documented and concludes with a brief summary. The volume has an extensive bibliography and good indices. Unfortunately the prospective reader must be warned that the volume contains a considerable number of minor errors, not all of which can be attributed to the printer.

There is a wonderful opportunity now for bird students to compare with this account their findings on the characteristics of other members of that great complex of Song Sparrow subspecies that range from the pallid little *saltonis* of the southwest to the blackish *rufina* of southern Alaska and the giant race *sanaka* of the Aleutian Islands. In fact, one of the important contributions of this work will prove to be its tremendously stimulating effect on ornithological research of many kinds.

The American Ornithologists' Union expressed the opinion of ornithologists generally when it awarded Mrs. Nice the Brewster Medal in 1942 in recognition of this study as the "most important work relating to the birds of the Western Hemisphere."

JOSSELYN VAN TYNE

SHORTER ARTICLES AND DISCUSSION

VARIATION IN PETAL NUMBER IN THE BLOODROOT, SANGUINARIA CANADENSIS

For some years in our course in genetics at Wooster we have carried on studies of variation in natural populations of certain plant species. The spring beauty, *Claytonia virginica,* has furnished unusually favorable material for a study of microevolution (Spencer, 1942). We herewith present material on variation in petal number in the bloodroot, *Sanguinaria canadensis,* collected biennially since 1926. Unfortunately the collection records for two of these years have been lost. One other year the short flowering period passed without records being taken. To the many students in his genetics classes who have aided in this project, the author is indebted.

Sanguinaria, belonging to the poppy family, is described in Gray's Manual as follows:

> Sepals 2. Petals 8–12, spatulate-oblong. Stamens about 24. Style short; stigma 2-grooved. Pod ellipsoid or fusiform, turgid, 1-celled, 2-valved. Seeds with a large crest.—Low perennial; its thick prostrate rootstocks sending up in earliest spring a palmate-lobed leaf with 1-flowered scape. Flowers white, handsome, the bud erect, the petals not crumpled.—Open rich woods; common. Apr., May.

The petal number is sufficiently large to give a workable morphogenic series and sufficiently small to make possible the securing of extensive data with reasonable expenditure of effort. In our latitude the plant flowers in late April and early May. The flowering period in a given locale is short, a week to 10 days. During this period there is a peak lasting for about 3 or 4 days, and it is during this peak that data have been secured. In northeastern Ohio populations of this species are quite common but discontinuous. These may consist of isolated patches of a few hundred plants scattered over an area of an acre or less to large colonies a half mile or more in length. The latter are broken up into concentrated subpopulations where plants are very numerous. The distribution is definitely related to the drainage systems, with colonies occupying the sloping, open-wooded banks along stream valleys. Thus many colonies average 20 to 100 yards in width and extend for considerable distances along these banks. Where the slope is more gradual the colony spreads out correspondingly.

We have made collections principally from two populations. The Overton Road population occupies a wide sloping meadow and open woodland at the fork between the Killbuck and Little Killbuck valleys in Wayne County, Ohio. This population covers an area roughly one-third mile long by one-fourth mile wide. The Little Apple Creek colony, the smaller of the two, stretches for about one-half mile along the steep banks on the eastern side of the valley, and varies in width from 20 to 100 yards, with tongues running up the ravines leading into the valley floor. These two colonies are approximately 4 miles apart.

Data are collected as follows: During the peak of the flowering period a group of workers, each with pencil and card, works through a colony, pulling off flowers, and counting and recording petal number. In this way the same flower can not be recorded twice. The group of workers varies from 5 to 20, and by working through the area covered by a population probably secures a better sample than one worker, even though he collected the same amount of data. By collecting on one day no area is depleted of flowers for re-seeding, as there are always many flowers yet in bud left. The method should have relatively little effect on the structure of the population.

TABLE 1

VARIATION IN PETAL NUMBER IN THE FLOWERS OF SANGUINARIA CANADENSIS. SUMMARY FOR SIX YEARS OF COLLECTING

Petal No.		4	5	6	7	8	9	10	11	12	13	14	15	21	Total
Year															
1926		2	1	8	16	835	24	15	18	26	7	10	2		964
1932		0	2	10	61	1,816	269	105	64	40	1	1	2		2,371
1934		2	5	25	165	4,965	785	493	296	212	34	10	2		6,994
1938		0	3	28	127	6,571	564	277	138	73	9	7	4	1	7,802
1940		6	6	28	189	11,315	669	288	182	135	15	5	3		12,841
1942	1	0	4	5	44	6,738	521	292	173	125	13	2	0		7,918
Total ...	1	10	21	104	602	32,240	2,832	1,470	871	611	79	35	13	1	38,890

In Table 1 a summary of all collecting for 6 years and for all areas is given. From this table it will be noted that the modal petal number is 8, with a mean lying between 8 and 9 and closer to 8. Extreme variants range from one flower with 3 petals to one with 21 petals. There are more than 10 times as many 8-petal flowers as the next most numerous class of 9 petals. The curve of variation is definitely skewed toward petal numbers above 8.

The data by years for complete collections from the two populations already mentioned are given in Table 2. From the totals, if we assume that the Overton Road sample, which is the larger, represents the theoretical distribution of variants for the species, a 2 × n table may be constructed for the Little Apple Creek population. Such analysis gives a chi-square which is highly significant. Thus on the basis of the total samples the two populations differ significantly in petal number. Furthermore, following the same procedure for collections for each year the differences are significant except for the 1942 collections, where the differences are of doubtful statistical significance.

TABLE 2

VARIATIONS IN PETAL NUMBER IN TWO POPULATIONS OF SANGUINARIA CANADENSIS

Petal No.	3	4	5	6	7	8	9	10	11	12	13	14	15	21	Total
						Overton Road Population									
Year															
1932		0	2	10	61	1,816	269	105	64	40	1	1	2		2,371
1934		0	1	8	46	3,473	648	378	237	172	27	8	2		5,000
1938		0	2	10	72	4,537	394	185	80	40	5	5	1	1	5,332
1940		1	3	15	129	4,337	371	149	84	62	7	2	0		5,160
1942	1	0	0	1	17	2,511	215	90	43	36	1	1	0		2,916
Total ..	1	1	8	44	325	16,674	1,897	907	508	350	41	17	5	1	20,779
						Little Apple Creek Population									
Year															
1934		2	4	17	119	1,492	137	115	59	40	7	2	0		1,994
1938		0	1	18	55	2,034	170	92	58	33	4	2	3		2,470
1942		0	4	4	27	4,227	306	202	130	89	12	1	0		5,002
Total ..		2	9	39	201	7,753	613	409	247	162	23	5	3		9,466

From the data in Table 2 combined with field observations, certain tentative conclusions may be drawn. These two populations differ in respect to the distribution of variants in petal number when collections over a period of years are considered. The Little Apple Creek population gives relatively larger numbers of low petal number types and the Overton Road population relatively larger numbers of high petal number types. However, such a conclusion might well be missed by taking collection records for only one year (see 1942). These larger populations are in turn made up of smaller subgroups. It is the usual thing to find flowers with more than 8 petals together in small subpopulations a few feet or yards in diameter. Some of these plants belong to clone cultures, as the rootstocks branch. Also flowers of less than 8 petals tend to occur close together. But there is no tendency for flowers of more than 8 and flowers of less than 8 petals to be associated. It would seem likely that different genetic factors condition high petal number from those conditioning low petal number. Furthermore, since variants of 9, 10 and 11 petals are often grouped together the exact petal number is probably influenced by modifying factors, genetic and/or environmental. In fact, transplantation of some of the rootstocks and subsequent flowering have indicated that both genetic and environmental modifiers are at work. Some years ago a bloodroot flower with over 60 petals was brought to the laboratory. This came from a plant found in the wild and transplanted to a garden. It was undoubtedly a mutant to a "double" form and distinct from the factors dealt with in our studies.

The collections for 1942 both from Overton Road and Little Apple Creek show one peculiarity in common. In both populations the number of variants below 8 petals is very low when compared with other years. There has been no corresponding drop in the number of variants of more than 8 petals. It seems hardly likely that both of these populations, quite distinct from one another, should suddenly fluctuate in their genetic makeup so markedly and in the same direction in the same year. Rather it would seem more plausible to interpret the results in terms of some combination of factors in the growing season, perhaps temperature and moisture relationships, conditioning a phenotypic suppression of low petal number. However that may be, the case emphasizes the importance of studies based on collections made from more than one growing season in establshing the facts concerning variation between two populations. During the course of these investigations we have noted other morphological changes, particularly difference in petal shape, in which the distribution indicated a genetic basis.

It has not been deemed either necessary or expedient to present any extended statistical analysis of this material. Such analyses imply a finality which the nature of the data almost certainly does not justify. In this case it seems likely that we are dealing with genetic factors which form microgeographic races (Epling and Dobzhansky, 1942). It would be of interest to secure data from the other parts of the geographic range of Sanguinaria for comparison with these local populations. This has been done for sepal number in *Hepatica acutiloba* by Anderson (1936). It is realized that we present here only a small and imperfect fragment of the pattern of variation in one species as it occurs through the years.

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A CYTOLOGICAL STUDY OF THE GENUS SORGHUM: SUBSECTIONS PARA–SORGHUM AND EU-SORGHUM[1]

THE genus *Sorghum* includes species with haploid chromosome numbers of 5, 10 and 20. Snowden (1936) has divided the genus, on a morphological basis, into two subsections: Para-sorghum and Eu-sorghum. All the species reported to date in the subsection Para-sorghum have a haploid chromosome number of five. Excepting *S. halepense* ($n = 20$), all the species in the subsection Eu-sorghum have a haploid chromosome number of 10. According to Snowden (1936), although no evidence is offered, the species of the subsection Para-sorghum have played no rôle in the evolution of species in this genus with higher chromosome numbers. The data from this preliminary cytological study suggest that the separation of the species into two groups appears to be a valid one. Indeed, there is reason to believe that the separation may be greater than implied by the subsectional status of the two groups.

The following species were grown at the University of Minnesota, St. Paul, and the University of California, Berkeley: *S. dimidiatum, S. versicolor* and *S. purpureo-serecium* (Para-sorghum); and *S. vulgare, S. sudanense, S. halepense* (Eu-sorghum). Panicles were fixed in a glacial acetic acid-alcohol solution (1 : 3). Smear preparations were used throughout with acetocarmine as staining agent.

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[1] The main part of the work for this paper was done at the Division of Agronomy and Plant Genetics, University of Minnesota, St. Paul, during a research assistantship (1941–42). The author wishes to express his gratitude to Dr. C. R. Burnham, whose suggestions and criticisms throughout the work were invaluable.

The chromosome complements of the species in the subsection Para-sorghum were morphologically similar in all phases of meiosis. No marked differences were evident so that any one complement would have been indistinguishable from the others. The chromosome complements of the species in the subsection Eu-sorghum were likewise morphologically similar in all phases of meiosis and, excepting chromosome number, no marked differences in morphology were evident. However, there were great differences in many characters between chromosome complements of the two subsections.

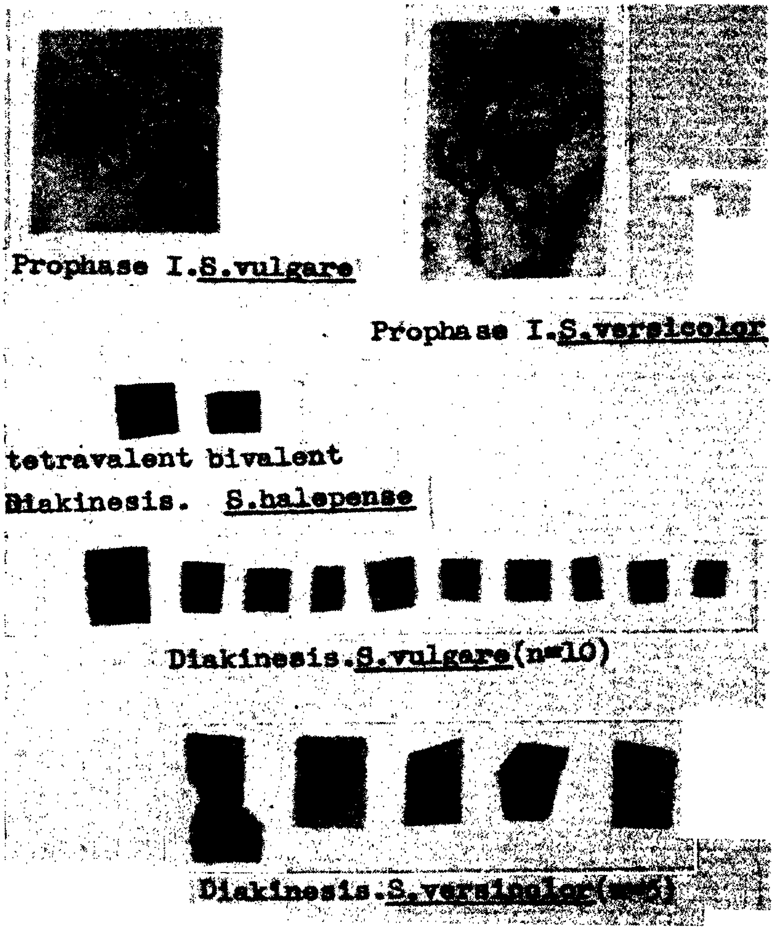

Fig. 1.

In the subsection Para-sorghum, the chromosomes at prophase

I stained uniformly throughout with acetocarmine. However, the chromosomes were so long and entangled that it was extremely difficult to determine chromosome lengths with assurance. These chromosomes appeared to be much longer than the familiar chromosomes of *Zea mays* at the same stage. The chromomeric structure was very clear.

The chromosomes of the species in the subsection Eu-sorghum at prophase I did not stain uniformly with acetocarmine. The stain tended to accumulate in the regions adjacent to the centromere. No attempt was made to determine the extent to which the selective staining was restricted to definite lengths of each chromosome arm. The chromosomes at prophase I were much shorter than those of the subsection Para-sorghum. The relative chromosome lengths in *S. vulgare* have been reported by Longley (1937). The chromomeric structure was not very clear, but close examination revealed the presence of chromomeres.

An outstanding morphological difference between chromosome complements of the two subsections was found in the nucleolar chromosome at prophase I. In species of the subsection Para-sorghum, the nucleolar chromosome was terminally attached to the nucleolus. The region of attachment was marked by a heteropycnotic, spheroidal bulge (not a satellite), separated from the remainder of the chromosome by a narrow, non-staining band. In the species of the subsection Eu-sorghum, the nucleolar chromosome was attached to the nucleolus at an intercalary point which did not appear to be morphologically distinguishable from the remainder of the chromosome.

The chromosome complements of the two subsections still displayed striking differences in morphology and size at diakinesis. It was possible to see the internal structure of the chromosomes of the species in the subsection Para-sorghum because of their relatively large size. These chromosomes at diakinesis were 10 to 15 times longer and 2 to 4 times thicker than chromosomes of the species in the subsection Eu-sorghum. It was not possible to see any internal structure in the chromosomes of the latter subsection because of their relatively small size. Again, all the chromosome complements within one subsection appeared strikingly similar at diakinesis.

At no time were multivalents observed in the species of the subsection Para-sorghum. Both *S. vulgare* and *S. sudanense* (Eu-sorghum) appeared to be diploid in that only bivalents were observed. However, univalents, bivalents, trivalents and tetravalents were found in *S. halepense* (n = 20). No chromosome associations higher than tetravalents could be definitely established in this species.

The chromosome configuration attached to the nucleolus in diakinesis in *S. halepense* was either a bivalent or a tetravalent. The maximum number of tetravalents observed in a single pollen mother cell was five. The numbers of tetravalents per p.m.c. ranged from zero to five. These data are based on 500 p.m.c. obtained from plants originating in Oklahoma and South Carolina. However, there is no reason to conclude that five tetravalents represent the total possible number of tetravalents nor that the same chromosomes are always contributing to the number of tetravalents observed.

The tribe Andropogoneae includes the genus *Sorghum* and allied genera. It was considered probable that there were species in the tribe Andropogoneae which have a chromosome complement not a multiple of ten but of five. No such chromosome number had been reported in the literature. Of the species examined, *Hyparrhenia hirta* was found to have a haploid chromosome number of 15. Incidentally, a reciprocal translocation was found in this species.

DISCUSSION

The cytological evidence suggests that the division of the genus *Sorghum* into two subsections by Snowden (1936) on a morphological basis is not only sound but a natural one. If such striking differences in chromosome morphology as are found between species in the two subsections are significant, then the species in the subsection Para-sorghum have indeed played no rôle in the evolution of species in this genus with higher chromosomes (Eu-sorghum). Taxonomically, there appears to be no doubt that these two subsections seem to belong in the one genus. Although the data are still meager, there is reason to believe that the two subsections may merit separation into two genera. No hybridization occurs between species in different subsections (O'Mara, unpub.).

Cytological and preliminary breeding data indicate a very close relationship among the species of the subsection Eu-sorghum. Excepting for chromosome number, *S. halepense* is essentially different from other species in this subsection only in that it is a perennial while the others are annuals. There is no doubt that this species is a polyploid, but it is not definite from cytological data whether *S. halepense* is an auto- or allopolyploid. Longley (1932) suggests that *S. halepense* is an autotetraploid. Karper and Chisholm (1936) conclude from their data that more than a mere doubling of the chromosome number resulted in the production of the polyploid species. This conclusion may find confirmation in that observation that the possible range of tetravalents (0 to 10) was not found in *S. halepense.*

Huskins and Smith (1932) conclude from data on somatic chromosomes that *S. halepense* is an allotetraploid, the product of a chromosome doubling in a hybrid between a species of *Sorghum* with a haploid chromosome number of 10 and a species in the tribe Andropogoneae, presumably with a haploid chromosome number of 10. In a subsequent paper dealing with the meiotic chromosome in the genus *Sorghum,* Huskins and Smith (1934) report tetravalents and hexivalents in *S. vulgare* and hexivalents in *S. halepense.* Considering all the data, they suggest that the basic chromosome number for the genus *Sorghum* may be seven and not ten. However, no multivalents were observed in *S. vulgare* or *S. sudanense* ($n=10$); no hexivalents were found in *S. halepense* ($n=20$) but univalents, bivalents, trivalents and tetravalents. It is more probable that the basic chromosome number for the genus *Sorghum* may be five. It appears to be more than coincidence that the subsection Parasorghum has a haploid chromosome number of five, the maximum number of tetravalents observed in *S. halepense* is five, and a species, while not closely related, in the tribe Andropogoneae, *Hyparrhenia hirta,* has a chromosome number ($n=15$) which is a multiple of five and not ten or seven.

There still remains the problem of the origin of *S. halepense.* Breeding and cytological data indicate a very close relationship with the species of *Sorghum* with a haploid chromosome number of 10. It is very likely that one of these species was involved in the production of *S. halepense.* However, there are no clues concerning the other putative parent involved in the supposed hybrid which gave rise to *S. halepense.* There is no reason to assume that this putative species belongs to a genus other than *Sorghum,* as was suggested by Huskins and Smith (1932).

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THE NEMERTEAN GORGONORHYNCHUS AND THE FLUCTUATIONS OF POPULATIONS[1]

IN a paper (Wheeler, 1942) discussing the significance of the recent discovery of nemerteans with a type of proboscidial apparatus heretofore undescribed, the naive suggestion is made that the branched type of proboscis peculiar to Gorgonorhynchus may have originated within the past forty years from a form with a simple tubular organ. The only grounds for this conclusion were that two species of the new form were found almost simultaneously on the coasts of Australia, India and Bermuda and that they had not been reported by earlier investigators who had made collections in the same regions.

It was considered remarkable that a species now plentiful on the shores of Bermuda was not found either by Verrill or by Coe, who had searched the same localities near the beginning of the present century. Considering also the circumstance that certain other species of nemerteans which were found at Bermuda forty years ago have not been seen recently, Wheeler infers that one of them may have been the "mutation mother-species of Gorgonorhynchus by development from the eggs." What a thrill it would give to students of evolution if such an inference could be substantiated. But since that seems to the writer unlikely of realization, a simpler explanation and one more in harmony with the behavior of littoral populations may be appropriate.

There is, of course, a possibility that the species has but recently arrived at Bermuda on the bottoms of ships, as suggested by Zimmerman (1943) and also considered by Wheeler, but such a distribution of a burrowing worm with the habits of Gorgonorhynchus seems improbable. More seriously to be considered is the factor of chance. The combined intertidal shorelines of all the Bermuda islands extend for more than fifty miles, along which are innumerable stones that would form suitable protection for the nemertean. It is safe to say that relatively few of these stones have even yet been lifted to expose the treasures which may lie beneath them. Perhaps it was only by a mischance that neither Verrill nor Coe happened to look under just those stones which concealed a worm with such an aberrant structural modification that neither could have failed to notice if such a worm had been seen. The writer is unwilling to admit that human eyes are any sharper to-day than they were at the beginning of the century.

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[1] Contributions from the Scripps Institution of Oceanography of the University of California, La Jolla, New Series, No. 218.

It is obvious that the chance of finding a representative of a species will increase rapidly as the number of individuals in the population becomes greater. And it would be unusual if any population remained constant in numbers. Every observer of long experience has witnessed many such fluctuations in abundance from year to year.

Populations wax and wane; periods of abundance are followed by others of relative scarcity or complete disappearance (Clements and Shelford, 1939; Coe and Allen, 1937). Such periodicities are as characteristic of the populations of littoral worms as of other organisms. They are so familiar to all biologists that it seems unnecessary to mention specific examples.

New species of animals and plants are being discovered in familiar localities every year; numerous individuals of the new type may appear suddenly and later disappear with equal rapidity. Dominant populations may be replaced by others, quickly or over a period of years. An increase in one locality may accompany the decrease or the complete disappearance of the same species in certain other regions.

Some of the described species have as yet been reported on but a single occasion. Their discovery may have been due to the circumstance that one or more individuals wandered from the usual habitat of the species. As the population increases a wider dispersal is likely to ensue. As an extreme example may be mentioned a species of nemertean of which two individuals, each more than a foot in length, were found on the shore at Woods Hole, Mass., during an extremely low tide in June, 1894. Their morphological peculiarities were such as to make them the type of a new genus (Parapolia). In spite of persistent search in the same locality and elsewhere during many of the intervening years, no additional representatives of the species have been found. And yet it seems not improbable that numerous individuals are living somewhere in the vicinity, perhaps somewhat below the low-water mark, for in such situations burrowing animals are difficult to obtain.

It may be assumed therefore that "Polia or Eupolia," which is mentioned by Wheeler as the possible "mutation mother-species" of the form with branched proboscis, is not "moribund" and it may be confidently expected that it will appear again in full vigor and quite unchanged by the allegation that it is at present masquerading in the guise of Gorgonorhynchus.

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THE
AMERICAN NATURALIST

VOL. LXXVIII March–April, 1944 No. 775

GONAD HORMONES AND SEX DIFFERENTIATION[1]

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MY worthy predecessor, Professor W. R. Coe, of Yale University, in his retiring address before Section F in 1939 charmingly paved the approaches to the present discussion. Speaking on "Divergent Pathways in Sexual Development" (Coe, 1940), in his inimitable manner, Professor Coe unfolded for us the devious pathways utilized by invertebrates to attain the same end, *i.e.*, the reproduction of the species. He painted the picture of ingenious mechanisms employed, the manifold deviations from a common pattern, the oscillations from one sexual state to the opposite, and even the dangerous positions of the lowly male when his functions had been fulfilled; the end might be oblivion, a change to the opposite sex, death from natural causes or decapitation by the female in a fit of psychosis.

Just prior to utter exhaustion from the beautifully executed synthesis Professor Coe recalled that there were vertebrates, and that they employed certain hormonal mechanisms in their reproductive economy; and he attempted to bridge the gap between sex-determining mechanisms dependent upon gene action alone in invertebrates and the current conception of hormonal influences in sexual differentiation in the vertebrates; it rather left the vertebrate sexologists desirous of more pabulum. Since investigations on hormones have been so intensively pursued for the past decade, impelled onward by the magnificent performance of biologists and biochemists in isolating, testing, purifying, analyzing and finally synthesizing many of the sex hormones, and since especially the writer has recently published observations and conclusions that to many are either unorthodox or downright heresy, this presentation may be regarded as the promised further discussion of the general aspects of the problem pertaining to the role played by sex hormones in sex differentiation (Moore, 1943).

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[1] Paper by retiring vice-president and chairman of the Section on Zoological Sciences, American Association for the Advancement of Science, December, 1943. Personal researches have received support from a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of The University of Chicago.

Relatively recently a number of excellent reviews or synthesizing articles have dealt with the question of the role of sex hormones in sexual differentiation; these have applied to special groups or classes of vertebrates or have dealt with such special topics in the field as sex reversals, modifications of sex characters and others; but in view of their comprehensive documentation it is unnecessary to attempt complete coverage of relevant literature (Danforth, 1939, 1942; Domm, 1937, 1939; Willier, 1939, 1942; Witschi, 1939, 1940, 1942; Humphrey, 1942; Greene, 1942; Burns, 1938a, 1942a, b). A consideration of these reviews throws upon the individual a seemingly impossible task of clarifying existing opinions as to the meaning or significance of a vast multitude of factual materials. Confusion exists not only from lack of similarity in objective results or real differences in interpretation, but also mere terminology itself introduces considerable difficulty. Thus in articles presented in one symposium we may contrast the two following general statements:

> The most important general result evolving from recent work on sex determination in amphibians is probably a realization that under normal conditions the *sex hormones*[2] have relatively little, if anything, to do with primary sex differentiation, and that the inductor substances, which play their roles at earlier stages of the ontogenetic process than the sex hormones, belong in a separate class of chemical materials (Witschi, 1942).

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[2] Italics, mine.

From another:

> The actual mechanisms whereby one sex component predominates over the other in the differentiation of the gonad appears to be endocrine in nature. This is clearly indicated by the sex reversal effects produced by the *sex hormones*[2] injected. What the genes actually control physiologically, therefore, is the intensity of hormone secretion. The gonad component with the relatively greater intensity of hormone secretion determines the direction of sex differentiation (Willier, 1942).

Despite these seeming contradictions, however, it appears that the authors may actually hold quite similar opinions relative to the subject. Differences in usage of the term "sex hormones" have been the cause of much misunderstanding.

Since the first demonstration of an internal secretion for the testicle by Berthold in 1849 we have spoken and written of the testis hormone, or male sex hormone. Steinach early in the present century firmly implanted into the literature the terms male, or testis hormone, and the female, or ovarian hormone, and endowed each of these with the two cardinal functions of stimulation of homologous tissues, and inhibition of tissues or end organs of the opposite, or heterologous sex; inhibition of the opposite sexed gonad was also believed to occur. As advances were made in the isolation of the respective active substances from the gonads it became apparent that several substances were obtainable from female tissues or fluids that exerted typical feminizing effects and from male tissues or fluids different pure chemical substances were prepared that exercised masculinizing reactions. These substances have come to be designated as estrogens and androgens. When the pure crystalline substance testosterone was prepared from testis tissue extracts and the parent substance was combined with other substances to produce the score or more chemical androgens, interests naturally centered on their biological activities. In the numerous instances wherein responses to androgens were given by a female end organ the tendency arose to speak of the estrogenicity of androgens, and similarly the androgenicity of estrogens.

With all the tremendous advances in our knowledge we still do not know the constitution of the substance, or substances, secreted by the sex glands as their internal secretion, but presume the testis hormone to be somewhat similar to testosterone, or some compound of it, and the ovarian hormone to be similar to estradiol. We do not know whether the same hormonal substance is secreted by the different species, and there is still great uncertainty as to the period in ontogeny when hormone secretion begins, or when it becomes effective in the organism. Finally, we are not certain whether the gonad secretes more than one estrogen or androgen, but in some instances there is good evidence that the gonad may secrete both androgenic and estrogenic substances.

Recognizing all the attendant uncertainties and difficulties involved, however, it is of interest to consider the question of the role of sex hormones in sex differentiation, and particularly to examine somewhat critically the current viewpoints on the subject and survey the evidence for them. For the sake of clarity it may be stated that this discussion will be confined largely to the steroidal group of hormones that exercise such functions as are usually described under the terms androgenic and estrogenic.

The present generally accepted interpretation of sexual differentiation involves the notion of a genic mechanism in which, by virtue of the character of the parent germ cells, a dominance of the male-producing or female-producing set of factors is established. Although factors for both maleness and femaleness are present the more powerful set predominates over the lesser and gives character to the gonad as it develops into a testis or an ovary. An integral part of the sex equipments is the two sets of embryonic ducts—the male or Wolffian, and the female or Mullerian, duct—and other accessory organs. When the dominant set of sex factors expresses itself in the gonad as testis or ovary, specific hormones are believed to be secreted by the gonad, and the development of the duct system and accessory sex characters is believed to be dependent upon the action of the hormone secreted by that gonad; the hormone would thus stimulate the homologous characters and inhibit the heterologous ones. Although enjoying wide acceptance there is very little substantial evidence to support this hormone interpretation aside from the case of the freemartin, which we may briefly consider.

In 1917 through the observations of Lillie (1917) it became known that twins in cattle experience fusion of embryonic membranes, together with fusion of allantoic blood vessels from the two embryos. This union of embryonic blood vessels, which permits an interchange of fetal blood between the members of the pair, is accompanied by a modification in the reproductive systems of females twinned with males, but not in any other twin combinations; no modification occurs in the reproductive system of the male partner. Presumably, a testis hormone secreted by the male is carried to the female partner and exercises its postulated double effect, *i.e.*, the male hormone inhibits the heterologous or female components of the developing female embryo, and stimulates the homologous or potential male structures. Thus the genetic female suffers inhibition, even recession, of the cortical portion of the ovary, and the medulla in many cases develops into a typical sterile testis; the Mullerian or female duct system is inhibited, and largely removed, and the Wolffian or male duct system is stimulated to develop, so that the unusual female (freemartin) becomes provided with an almost complete male reproductive system.

The remarkably clear and consistent analysis of this centuries-old freemartin problem, and Lillie's preferred interpretation of events on a hormonal basis (other possibilities were considered by him) at a period considerably earlier than the isolation of any of the sex hormones, represents both a masterful analytical investigation and the beginning of the conception that sex hormones play an important role during sexual differentiation. This work not only represents one of the milestones along the pathway to a better understanding of some of the basic phases of the biology of sex, but also it has served as a powerful stimulant and challenge to investigators in this field for more than a quarter-century, and the theoretical aspects still represent the preferred interpretation of events during sexual differentiation. We find in the conception the basis of an explanation of human hermaphroditic conditions (Young, 1937) as well as sexual abnormalities of many distinct grades occurring among the different classes of vertebrates (Ivy, Greene and Burrill, 1939; Burrill, Greene and Ivy, 1940). The conception also remains basic for interpretation of modifications obtained after experimental treatments of embryos with the more recently available chemical hormones.

Recent observations of the writer, after experimental treatment of embryos, presented difficulties in interpretation on the basis of the hormonal control of sexual differentiation, and the failure to duplicate the essential freemartin effects in the course of more than twenty-five years of repeated attempts appeared to warrant a critical reexamination of facts and theories that have accumulated during the intervening years. This appears to be especially needed for interpretation of results reported after treatments with chemical hormones. In our ardor to learn all the possible effects of a hormonal substance there is danger of fixedly attending to the powers of the given hormone and of neglecting to consider broadly the powers of the organism to show changes under unusual conditions, or after unusual treatments. All effects of introduced hormones are based upon organ responses, and we sometimes neglect to consider that a response depends as much upon capacities of organs or tissues to respond as it does upon the agent administered. Intensive attention to one substance, or types of substances, may cause us to conclude erroneously that the reaction is a specific one whereas it may possibly represent a response that may be induced by many totally different kinds of agents. It appears advisable, therefore, to momentarily back away from the immediacy of an experiment and attempt to inquire more broadly into the concept of the role of sex hormones in development.

Before entering into some detail on separate phases of investigation that have a bearing on the general problem, brief mention of somewhat similar conditions to that inherent in the fusion of membranes in cattle twins may be in order.

The character of the embryonic membranes in cattle appears to favor fusions between those present in the same uterus, and it might be presumed that other ungulates would show similar trends. The thousands of pregnant uteri of the pig examined each year in courses in embryology, where simple placentae may be under study, suggests that the usual necrotic ends of chorionic vesicles effectively prohibit fusion, and it is largely the exceptional side-to-side fusions which provide possible materials for study. Such were the types utilized by Miss Hughes (1927, 1929) in her study of a few cases of freemartin conditions in swine, as well as the single case of Hoadley (1928). Hughes points out a greater variability in the female modifications in fused pairs of heterosexual pigs than in cattle, and suggests that rather than complete cortical degeneration in the ovary the germinal epithelium retains considerable activity. Concerning such modifications as attend on blood vessel fusion between heterosexual twins Wislocki has reported two different cases in which expected results were not apparent. In twin cat fetuses fusion between fetal blood vessels of a heterosexual pair had no apparent effect upon the reproductive system of either sex (Wislocki and Hamlett, 1934); in the marmoset a few heterosexual pairs showing well-developed blood vessel connections did not show any trace of the modifications that are of usual occurrence in the female of cattle although the structural union was such as to expect them (Wislocki, 1939).

Such departures from the expected results suggest that among other things we should be careful in making assumptions that one species reaction will be the same in other species. We are yet unable to state whether cattle present some specific or special condition that favors the responses in the female of a heterosexual pair, but aside from the cow the freemartin type of influence is known to occur only occasionally in the pig and possibly goat.

Three general lines of approach have been employed to put to an experimental test the conceptions inherent in the theory of hormonal control of sex differentiation. These may be mentioned as evidence from (a) utilization of living tissues, (b) utilization of chemical hormones and (c) evidence provided by gonadectomy. These we may briefly survey in turn.

EVIDENCE FROM UTILIZATION OF LIVING TISSUES

In mammals, attempts have been made many times to simulate the basic freemartin conditions through the transplantation of developing gonads into opposite sexed hosts with the hope that successful testis transplants might introduce testis hormone into differentiating females. The reverse, or transplantation of developing female reproductive tissues into differentiating male hosts, sought to provide similar conditions in which developing female tissues would be subjected to male hormone secretions. A further procedure, employed to effect possible exposure of developing females to male sex hormones, was the method of parabiosis; this has been largely unproductive for the particular problem where mammals have been used, but in the case of amphibia it has been exceptionally productive in some phases which, as will be pointed out later, are largely inapplicable to the sex hormone conception of modification.

Approximately fifteen years ago the writer, using mammals, made numerous attempts to transplant testes as grafts into embryos of known age in rats and guinea pigs by opening the uterus and embryonic membranes.

These efforts, as well as attempts to introduce testis hormone into embryos by breeding females carrying active testis grafts, were unproductive with respect to our present problem of interest although they yielded important information for other problems. Parabiotic union between adult male and female, with attempts to breed the female of the pair, likewise failed to yield pertinent information; other workers have obtained offspring from females in parabiotic union with males without reporting sexual modification in offspring.

Transplantation of female embryonic reproductive tissues into intact male hosts of early ages provided more hopeful conditions for realizing modifications through circulating hormones. Buyse (1935) transplanted posterior portions of rat embryos of 11 to 14 days of gestation into the kidneys of adult males and females, and Moore and Price (1942) transplanted gonads, gonads and ducts, or the duct system alone, dissected from rat embryos from the 15th to 19th day post-coitum into subcutaneous pockets in post-natal hosts of age 4 to 30 days. On the study of gonadal development these two investigations are in agreement that as extremes, ovarian differentiation occurring in male hosts may result in normal appearing cortical tissue containing follicles, or in the conversion of medullary cords into testis-like tubules, but neither investigation provided evidence for a hormonal modification of gonad development; grafts resident in male or female hosts showed similar ranges in development. Duct differentiation, considered by Moore and Price, also failed to provide any response suggestive of a freemartin type of development, since neither obvious stimulation nor depression from heterologous hormones was in evidence.

In the bird the experiments of Willier (1927) would presume to provide adequate relations for embryonic hormone effectiveness on differentiating gonads and ducts. Chick gonads, either in the morphologically indifferent stage of development or the sexually differentiated stage (4 to 13th day incubation), were transplanted *to the chorio-allantoic membranes of hosts incubated for* 9 days. The successful grafts, recovered on the 18th day of host incubation, were therefore vascularized by host blood vessels, but, irrespective of the sex combination of host and graft, modifications in sexual differentiation were not noted; transplanted ovaries, vascularized by male host blood stream, differentiated normally, and female hosts carrying well-incorporated testis grafts in the membranes were not modified. These observations led Willier to conclude that "Hormonic sex-differentiating factors of the host embryo are either absent or, if present, they are ineffective in the modification of the engrafted sexual glands." The experiments of Dennis (1936) imposed even more rigorous conditions on both host and differentiating graft since not only were ovaries, prior to morphological differentiation, transplanted on the chorio-allantois of male hosts but they were accompanied by a testis graft on the membrane, and yet failed to indicate any male hormone influence; such associated testis grafts might be in actual contact with the differentiating ovary graft, and the testis graft might have originated from testis tissue known to be secreting hormone at the time of transplantation. Multiple testis grafts on the membranes failed to modify a female host supporting them.

Thus in birds and mammals, aside from differentiating embryos of pigs, cattle and possibly the goat, only negative evidence of modification of reproductive tissues (gonad or duct system) during the period of sex differentiation has emerged. Since response of tissues is the only criterion to indicate the presence of hormone it appears justifiable to suggest, also, that no evidence has been forthcoming to indicate hormone secretion by a differentiating gonad among these experimental procedures in which living tissues have been depended upon to supply hormone.

Amphibia have been the subjects of numerous experimental procedures devised to study the effects on sexual differentiation of hormones derived from living tissues. Such studies, carried on principally in this country by Witschi, Burns and Humphrey, have involved the transplantation of undifferentiated or sexually differentiated gonads into larvae of the opposite genetically determined sex, of the same or different species or race, as well as extensive experiments on parabiotic union of the same or opposite sexes. Recent very complete reviews of these studies (Witschi, 1939, 1940; Humphrey, 1942; Willier, 1939; Burns, 1938a) are recommended to the interested reader and the recall of outstanding results may serve for the present discussion. When the larval testis of a urodele, in the pre-primodial or primordial stage, is transplanted into a genetically determined female the developing host ovary undergoes such changes in the cortex-medullary components as to become a structural testis-like organ; a similar result may be obtained when heterosexual larvae are united in parabiosis. The cortex of the ovary suffers inhibition and the medulla is able to differentiate as a testis; the effective substance in the urodele appears to be carried by the circulatory system. Conditions in frogs and toads, while leading to a similar general interpretation that hormone-like substances are specifically produced in the two components of the sex gland ("cortexin" and "medullarin" provided by the cortex and medulla, respectively) that are mutually antagonistic, differ with respect to the intensity and distance over which the alleged substances are effective; in some species of frogs the substances are believed to diffuse through the surrounding tissues rather than being transported by the blood stream, and in the toad the range of effectiveness appears limited to the gonad itself. The medullary influence largely predominates over the cortex and effects transformation of ovaries to testes, but in certain combinations the cortical influence may predominate and lead to the formation of an ovary-like organ in the genetically determined male.

Our primary interest here is the bearing these phenomena have on the problem of the rôle of sex hormones on sex differentiation. For some years Witschi has been insistent in separating such effects as those reported above for larval amphibia from the true sex hormonal mechanism which, in amphibia, is evident at later periods in development; in most of these so-called "inductor" phenomena the duct system has not been involved. It is thought that these earlier modifications of gonads by living tissue may depend upon hormonal-like substances, presumably of a protein nature, entirely separate from the steroidal class of hormones with which we are especially concerned. Further consideration of this phase will be given below. On the whole, amphibia have demonstrated a very labile type of sex factor balance, and shifts from one condition of the gonad to another in addition to being effected by such experiments with living tissues, are likewise encountered in overripeness of eggs prior to fertilization, in treatments with lower or higher than normal temperatures, and probably in many other types of treatment; they, therefore, can not be regarded as specific influences but only as results that may follow many types of treatment. Hermaphroditism among amphibia is of relatively frequent occurrence and gametes of both types can function in fertilization although the genetical character of the original zygote is retained despite the reversal of gonad to the opposite sex type.

EVIDENCE FROM CHEMICAL HORMONES

The availability of pure chemical androgens and estrogens, as well as effective preparations of gonadotropic substances, has led to the wide use of such substances in studies on sexual development in the five classes of vertebrates. These experiments have yielded most interesting results on the capabilities of the tissues to respond to hormones, and to show modifications in sexual development, but the value of the information for an understanding, or analysis of normal processes controlling sex differentiation has been variously assessed. Numerous modifications in sex differentiation have been reported following treatments with the chemical hormones, but many failures to reveal modification under apparently similar conditions in other species are likewise recorded. Frequently the responses are non-specific, and may be recorded as paradoxical, and it is just possible that their greatest significance may lie in the emphasis on the capabilities of the organism to develop in devious ways under handicap; insults to developing tissues may demonstrate the well-recognized capacity to differentiate sexually in one of the two possible alternative manners, or to show a mixture of the two types.

Fishes: The young females of *Xiphophorus helleri* subjected to treatment with androgens shortly after birth are reported to show resorption of large eggs in the ovary, with ovaries gradually assuming testis-like appearance, but spermatogenesis was not noted (Witschi and Crown, 1937); others report 50 per cent. of the females developing into a male type organism with spermatogenesis indicated (Baldwin and Goldin, 1939). The minnow, *Phoxinus laevis,* exhibited a breakdown of the ovary with the assumption of a testis-like gonad (Bullough, 1940), whereas ovaries of the minnow, *Lebistes reticulatus,* showed suppression of growth and ovogenesis (Eversole, 1939, 1941).

In treatments with estrogens the male guppy, *Lebistes reticulatus,* experienced suppression of the male gonopodium and spermatogenesis was modified or suppressed. A mosaic of male-female characters was induced, as well as an ovo-testis; almost complete reversal of testis to ovary occurred (Berkowitz, 1937, 1941).

Responses of these types suggest a rather specific modification of the sexual state appropriate to the type of hormonal substance employed, or the induction of maleness by androgens and femaleness by estrogens. However, treatments of *Lebistes* with the synthetic steroid pregneninolone, which exhibits progestational activity and little or no androgenic activity, lead to an inhibition of female characteristics and a stimulation of the male gonopodium and in males a precocious maturation of the male elements (Eversole, 1939, 1941). Such responses suggest strong androgenic effects, but since this substance as usually tested on higher forms largely lacks such an action, it becomes of interest to speculate whether the responses in the organism are to those portions of the compound responsible for its androgenicity or merely to some type of chemical agent that disturbs the normal physiological processes in the organism. Witschi (1942) calls attention to unpublished observations of his student Crown (1941) that estrogenic compounds masculinized *Xiphophorus* females—a response just the opposite to expectation; ovaries regressed, and fins transformed into a gonopodium and the male sword began formation and growth. Baldwin and Li (1942) point to somewhat similar responses on the part of these females when treated with extracts from pregnancy urine; virgin females under such estrogenic treatment developed a male gonopodium, exhibited a male copulatory pattern and a reversed sex coloration and various stages of spermatogenesis were present. Without the use of any treatment, other than surgical removal of ovaries, the female fighting fish (*Betta splendens*) regenerated gonads of testis-like character, produced spermatozoa, and developed fins of the male type (Noble and Kumpf, 1937); and parturient *Xiphophorus* females are believed to frequently undergo sex reversal to the male condition, and produce spermatozoa, while living under natural conditions and without treatment (Essenberg, 1926).

This brief review of the unstable and changeable capacity of fishes to show different sexual states under treatment with hormones, or under other circumstances, leads one to question the significance of the androgenicity or estrogenicity of a substance to effect specific sexual responses in fish. Whereas some changes induced are possibly the expected ones in terms of the hormone substance employed, others distinctly are not; in addition, even more remarkable changes may occur without any treatment with hormonal substances. Perhaps the results are of value merely to emphasize the unstable sexual condition in many fish, and that disturbances of normal physiological processes under which the genic tendencies for sex express themselves, may be easily induced by hormones and perhaps by many other non-hormonal substances. When non-hormonal agents are employed in experiment with as great industry and interest as have the chemical hormones we may find expressions of androgenicity and estrogenicity from very unexpected substances or conditions.

Amphibians: Turning to the amphibia for an examination of effects of chemical hormones on sex differentiation we meet another conflicting set of results. In the main, when sexual modifications have been induced through such treatments, it is rather frequent that treatments of females with androgenic substances tend to modify these in the direction of maleness, and males treated with estrogens go over towards sexual differentiation of females. Thus androgenic treatment of females leads to the differentiation of a testis or testis-like gonad in *Amblystoma punctatum* (Burns, 1938), *Rana clamitans* (Foote and Witschi, 1939), *R. pipiens* (Foote, 1938) and in *R. catesbiana* when treated simultaneously with a gonadotropic agent (Puckett, 1939, 1940). Estrogenic treatments lead to feminizing influences on males and may convert the genetically destined testis to develop as an ovary, or ovary-like body, in *Amblystoma* (Ackart and Leavy, 1939; Burns, 1938b; Foote, 1940 and 1941), and in *R. catesbiana* if treated simultaneously with gonadotropins (Puckett, 1939, 1940); but when we recall similar modifications induced by living testicular and ovarian tissues, reported in the previous section, and the belief that the active agents in such transformations were substances of protein-like nature, one is in a quandary in attempting to evaluate the significance of the responses to the steroidal sex hormones.

In addition to these reversal effects that tend to conform to the nature of the hormonal substance—*i.e.*, androgens and maleness, estrogens and femaleness—other responses have been seen that do not follow such a pattern of correlation. *Rana pipiens* larvae treated during the indifferent stage with the synthetic steroidal compound exhibiting progestational effects (pregneninolone) are found later to be 100 per cent. males (Eversole and D'Angelo, 1943). Androgens may exert femininizing effects instead of the expected masculinizing ones (Ackart and Leavy, 1939; Burns, 1938b; Foote, 1940, 1941) and estrogens may induce masculinizing modifications rather than femininizing (Foote, 1938); and in several different experiments androgen or estrogen treatment may not lead to any modifications of the developing gonads. These diverse effects from chemical hormone treatment, coupled with known tendencies of overripeness of eggs to induce maleness, the tendency for lower than normal temperatures to favor femaleness and higher than normal temperatures to favor development of male tendencies in the gonads naturally introduces a quandary relative to the significance of these findings as indicating that specific actions of hormones are important in the differentiation of sex. Rather to be emphasized, it would seem, is the great liability toward sexual differentiation exhibited by the amphibia. The different conditions tend to suggest a lack of specificity of such agents and the probability that many other types of treatment that would interfere with ordinary physiological processes under which the expression of genic determination is to be seen might be equally effective.

Reptiles: Although reptilian materials have been less frequently examined for sexual modifications after treatment with sex hormones several reports are pertinent to the present discussion. Through the injection of chemical hormones into developing eggs of the lizard and turtle, and into young alligators shortly after hatching, such modifications during the course of embryonic development have been seen as to cause some investigators to explain sex differentiation on the basis of internal secretions occurring in the embryo. In the lizard, Dantschakoff (1938) demonstrated that estrogenic treatment during development induced modifications and that in both sexes cortical development in the gonad predominated at the expense of the medulla; on account of these femininizing tendencies, especially in males, she considered that the chromosomes produce a specific type of hormone which directs development of the indifferent gonad into the proper organ, testis or ovary. Risley (1940, 1941) noted also in the lizard that following androgenic treatment the medulla in the ovary was enlarged and became testis-like; this is regarded, however, as merely a secondary response of this tissue after differentiation of the gonad has already occurred under ordinary genic influences, hence hormones do not replace the induction mechanism inherent in the genic constitution. The accessory reproductive organs failed to exhibit any response. When he employed the recently hatched diamond-back terrapin Risley did not find a tendency for changes to follow in correspondence with the androgen or estrogen employed; gonadal changes were minor and both Wolffian and Mullerian ducts responded to treatment with androgens and estrogens. These results led him to subscribe to the notion that such hormones were not the agents controlling normal sex differentiation. Young alligators showed slight tendencies for stimulation of the cortex in both testes and ovaries by estrone (Forbes, 1937, 1939). The female ducts responded readily to both androgens and estrogens hence specificity of hormone action, inherent in the hormone concept of sex differentiation, appears not to hold for reptiles.

Birds: The treatment of the developing chick with chemical hormones (Wolfe and Ginglinger, 1935; Dantschakoff, 1936; Breneman, 1935; Willier, Rawles, Gallagher and Koch, 1937, 1938) has resulted in many types of modification in the reproductive system and some writers have seen in these responses evidence that *the control of sex differentiation under normal conditions is probably exercised by hormones secreted by the developing gonad*; a few of these conflicting results may be recalled.

In the chick, estrogens injected into eggs incubated for 48 hours, with embryos preserved on the 18th day of incubation, exert but little effect upon developing females; the ovary is not perceptibly modified and only with higher dosages the oviducts may exhibit hypertrophy with some increase in length of the right reduced oviduct. In developing males, however, marked changes appear following estrogenic treatments. Testicular modification differs materially in the right and left gonad since the right testis is usually unmodified excepting with the highest doses. The left testis exhibits all grades of differentiation from a normal testis to a gonad that is essentially ovarian in structure; the cortex reveals varying grades of stimulation and the medulla all grades of inhibition, or modification of the usual solid testicular cords into characteristically open and distended ovarian medullary cords. The oviducts of such males may persist partially or completely, the right duct being either slightly enlarged or greatly hypertrophied.

When androgens are utilized in the treatment the developing chick may exhibit a number of, and somewhat curious, responses depending upon the nature of the androgen employed (androsterone or testosterone), the genetic sex of the embryo and the dosage employed. Female chicks may respond to androgen treatment by a gradual degeneration of cortex and hypertrophy of medulla leading to an organ largely testicular in appearance; even the normally reduced right ovary may reveal hypertrophy of the medulla, hence the female chick is highly modfied in the male direction. The left oviduct may be reduced to a short rudimentary ostial portion while at the same time the right oviduct, normally reduced or absent, may be preserved and show a great increase in length. Male chicks treated with androgens revealed gonads that were only slightly reduced in size when the androgen was T-propionate, but when the androgen employed was androsterone the testis was almost completely changed over to an ovary. The left testis responded by cortical hypertrophy and testis cords were changed to resemble ovarian medulla. Thus it follows that the cortex of the genetic ovary is *inhibited* whereas its homologue in the genetic testis is *stimulated.*

The oviducts in males treated with the androgen T-propionate are not preserved but those in males treated with androsterone not only persist but may also exhibit a great increase in size. Further inconsistencies appear in that the oviducts, in genetic females treated with androgens, may show in the same embryo a reduction in the left oviduct and a stimulation in the right one.

Thus, these readily produced responses in developing embryos treated with chemical hormones are of very great interest in revealing the capacities of genetically determined sexes to exhibit characteristics belonging to the opposite genotype, but to apply the experimental results to normal development as an indication that sex differentiation is controlled by androgens or estrogens secreted by the genetically determined gonad would appear to be an impossible task. The differences seen in the two sexes do emphasize the power of the inherent genetic constitution to regulate the capacities for response on the part of the tissues to the substances introduced. But in the estimation of the reviewer they cannot be taken as evidence either that sex hormones are involved in the differentiation of the sexual equipment, nor indeed as evidence that the gonads are actually secreting. It will be recalled that Willier and Yuh (1928) have shown radical modifications in sexual differentiation in chicks that have carried muscle, or thyroid, grafts on chorio-allantoic membranes; and that even mere chilling of eggs increases atypical sexual modifications. These authors accounted for modifications described by Minoura

(1921), and attributed by him to sex hormones, as non-specific effects probably unassociated with gonadal hormones. Willier (1927) has emphasized the lack of influence on differentiating gonads exposed to the constant circulation of an opposite sexed host, hence to any circulating hormones that would be present in the event the intact host gonads were secreting.

It has been shown that chicks treated with gonadotropic substances during embryonic stages experience an increase in size of gonads but fail to give evidence for hormone secretion (Domm and Dennis, 1937); following treatments begun at very early periods, and also at later periods, no hypertrophy of Wolffian or Mullerian ducts appeared. Had the gonads been capable of secreting hormones at such periods, and especially since direct application of androgens and estrogens have proved these structures capable of response, duct reactions should have indicated it, hence it is suggested that the gonads of developing chick embryos are not secreting hormones; gonadotropic treatment of chicks immediately after hatching does clearly reveal the capacities for gonadal hormone secretion hence this capacity to respond must be attained sometime around the period of hatching. The reproductive systems are already well developed, however, hence sex hormone secretion by the gonads could not well be presumed to have been operative around the 10th day of incubation and earlier, as would be required, were they made responsible for controlling differentiation of sex ducts.

Mammals: The developing mammal has also been subjected to treatments with chemical hormones and sexual modifications have been described in the treated mouse, rat, guinea pig and opossum (Dantschakoff, 1937; Burns, 1939; Greene, Burrill and Ivy, 1939, 1940, 1942; Hamilton and Wolfe, 1938; Raynaud, 1938; Turner, 1939; Moore, 1941). Great variability in the number and character of responses has been pointed out. Strikingly absent have been modifications in the character of the gonads during their differentiation; it would almost seem as though the genetic mechanism for sex differentiation was markedly stronger than exists in the lower vertebrates, and that the gonads have gradually lost their great lability, or power of potentially different developmental capacities, as evolution has advanced. Neither the cortex nor medulla in any of the species cited has shown a definite change from normal development when subjected to estrogens and androgens. Testes in some cases have suffered some interference with their normal growth rate and have failed to descend into the scrotum, frequently in association with enlargement of duct portions believed to interfere with descent; ovaries in some cases appear to reside in somewhat more posterior positions as if there was the testicular tendency to backward descent. In no case, however, has an ovary, developing under the influence of androgens, shown any tendency to respond as did the freemartin ovary, by cortical degeneration and medullary development.

Duct and accessory reproductive organs have shown decided modifications after treatments with chemical hormones but in the aggregate the responses have been too heterogeneous and non-specific to suggest any credence in the belief that the developing gonad secretes similar substances that account for normal development. Thus the responses noted earlier in the investigations suggested evidence that would fit the postulates for specific action of hormones on duct development, since treatments of pregnant rats and mice with androgens was followed by the retention in newborn females of male or Wolffian ducts. The second postulated function for the hormone was not evident, however, since the female reproductive system, aside from the distal third of the vagina, was normal whereas it should have been inhibited by the androgens; oviducts and uterine horns were entirely normal. It is clear that freemartin effects, as they apply to duct systems, were evident only in part. A greater unconformity was encountered when pregnant females were treated with estrogens and developing females showed the unusual retention of Wolffian or male ducts, to an extent similar to that which followed treatments with androgens. In developing males, also, some features suggested conformity with the hypothesis of hormone control of duct development, whereas others failed to do so.

In a high percentage of treated pregnant mothers placental damage was marked (high fetal death and resorption just prior to parturition). It is conceivable, even probable, that such placental injury may of itself engender abnormal development and that atypical conditions might possibly be entirely separable from specific actions of the hormones employed. Such uncertainties were avoided by the utilization of the developing marsupial as the experimental subject. The opossum at birth is structurally undifferentiated as to sex, with gonads indistinguishable as ovary or testis, with large Wolffian (male) ducts functioning as urinary ducts, and with Mullerian or female ducts showing first appearance on day three, and requiring until about day ten to attain their urogenital sinus connections. During these periods of development, and later, opossum pouch young were treated daily with androgens and estrogens. Androgenic treatment caused but little stimulation of male (Wolffian) ducts, and would not preserve their posterior connections in females; persistence of portions of the Wolffian ducts, however, was more prevalent than in normal female development. In developing females these androgenic treatments not only failed to inhibit and eliminate the female ducts, as would be anticipated, but they caused marked precocious stimulation and induced uterine gland formation. It was noted that both the male and female duct systems, in either the genetic male or female, could respond to androgens or estrogens. It has been noted by Burns, however, that sufficiently weak doses of hormones can be utilized as will produce stimulation of the homologous duct system without stimulation occurring in the heterologous ducts; heterologous inhibitions were not noted. It will be of much interest to see how far this type of reaction may be carried, and to determine whether it has greater significance than a different threshold of response in the two duct systems.

One feature was encountered in these experimental procedures that is believed to be of special importance. It was found that when litter-mate males and females were treated with androgens during the early stages in formation of the Mullerian (female) ducts, the responsiveness of this duct was markedly different in the two sexes; daily treatments with the same dose of androgens, up to approximately day 30, revealed that the diameter of the lumen of Mullerian ducts in females was 100 times that in males. This fact emphasizes that the genetic constitution of the organism, irrespective of our notions of morphological homologies, clearly determines its capabilities of response to inciting agents; certainly the capacity of the Mullerian ducts to respond to the same agent is totally different in the two generic sexes, and it focuses attention upon the importance of genetical sex determination. Burns has repeatedly pointed to instances in which differential responses of the same structure occur in the two different sexes.

Since the capabilities of developing structures to respond to androgens and estrogens were so apparent, young male and female opossums were subjected to treatments with gonadotropic substances in an attempt to determine whether developing gonads were secreting sex hormones, or were capable of doing so (Moore and Morgan, 1943). When the duct system in females, and prostate gland development in males, were employed as indicators for estrogens or androgens liberated by a stimulated gonad it was found that evidence for testicular hormone secretion was obtained at an age of approximately 60 days or older, whereas no evidence was had for ovarian hormone secretion until subsequent to day 100; some evidence has more recently been obtained for an earlier testicular response when Cowper's gland is utilized as indicator for androgenic substances (Rubin, 1943), but all the evidence thus far available suggests that the developing gonads are incapable of secreting sex hormones when subjected to treatments that should cause them to secrete, if capable, until periods much later in development than sex duct differentiation.

The problem of the stage in development at which different portions of the reproductive system are capable of responding to chemical hormone influence is recognized. The problem has recently been investigated by Price and Ortiz (in press) in young rats. With standard dosage and constant length of treatment, and age at beginning of treatment as the variable, it has been found that male tissues in general reveal a low responsiveness to androgenic treatment at birth, and that sensitivity increased rapidly to a peak around day 30 when normal males usually reveal changes leading up to puberty; similar conditions for responses of female tissues to estrogens was also noted, but the initial response to treatment was relatively greater in females than in males. Hormonal secretion by the gonads, as a response to gonadotropic treatments, also exhibited a gradual increase from birth up to three or four weeks of age. In the investigations of Smith and Engle (1927) it was pointed out that pituitary stimulation of ovaries was readily evoked around day 20 but much less evident prior to this period. These, and many other, collective evidences suggest that the province of hormonal control over reproductive tissues, and functions, is properly one that emerges with gradual development around the natural age of puberty, and other indications equally suggest that hormonal actions are probably not normal controlling agencies during early establishment of the tissues that will later be the responding end organs when the hormonal mechanism becomes established.

EVIDENCE FROM GONADECTOMY

The final body of evidence to be discussed for its bearing on the relation of sex differentiation to hormones, and the question of the onset of hormone secretion by gonads, will be drawn from normal prepuberal development, and especially from the effects of early gonadectomy.

The general features attendant on the attainment of puberty are fairly well known. The mention of a few specific events, however, may aid in more sharply focussing attention on the earlier evidences for sex hormone secretion. Such events, that depend upon gonad hormone secretion, as growth of breast tissues and the first menstruation afford definite signs of approach to puberty in the human female some years after birth. The first vaginal introitus occurring in rats and mice, at ages variable in colonies and strains from day 35 to 65, indicate the first outpouring of hormones in sufficient concentration to effect this cyclic event. Young male rats about 35 days of age reveal the early signs of secretion in seminal vesicles, which is definite evidence for the attainment of hormonal secretions sufficient to accomplish this stage in development. Guinea pigs first produce coagulable ejeculates (indicating prostate and seminal vesicle function) around day 20 (Sayles, 1939). Such data provide us with the earlier indications in normal development for detectable beginning of sex hormone secretion, and numerous experimental treatments with gonadotropins clearly demonstrate capabilities of gonads to secrete earlier, or more intensively, than occurs in normal development.

Gonadectomies performed at very early periods should by the removal of all possible gonad hormone secretions provide further evidence relative to hormone secretion. Wiesner (1935) castrated male and female rats at birth and considered that he was able to demonstrate hormonal influence from about the 10th day after birth in the male, but not until the approach of puberty in the female. On the basis of these and other procedures he was one of the first to question the correctness of the conception of the hormonal control of sex differentiation, and developed the hypothesis that females differentiate without the influence of sex hormones whereas the male requires testis hormone to effect its differentiation. This "monhormonic" theory visualized all reproductive differentiation to take place in the female direction if hormones were not present, and that under the influence of testis hormone, development was modified into the male pattern. Price (1936) castrated male rats at birth and, on the basis of prostate gland and seminal vesicle histology, was able to note deficiencies in male hormone as early as the 11th day; and in unpublished observations of Cieslak, who employed weights of epididymis in young rats as the indicator, deficiencies are observable by the eighth or ninth day after birth. Collectively, these findings suggest that testis hormone secretion in the rat is apparent very shortly after birth. In any event it is to be expected that hormone secretion is a gradual development, perhaps beginning at a very low intensity and gradually becoming stronger, and it is not until sufficient concentrations are present to affect responding tissues that it becomes evident. We should, however, keep clearly in mind that the gonads are capable of hormone secretion prior to the time it can be detected normally, since treatments with gonadotropic agents can incite secretion considerably earlier than it is apparent in untreated animals.

The time in development at which gonadectomy can be accomplished in placental mammals is thus far limited to post-natal ages but in the marsupial, although also limited to a post-natal period, gonadectomy can be accomplished during stages in development that are present in placental mammals considerably earlier than birth; in effect, such a procedure is the equivalent of "embryonic castration." In the opossum, ovaries and testes have been removed on day 20 while the young are confined to the marsupial pouch firmly fixed to the nipples (Moore, 1943). The prostate gland in males and the reproductive tract in females, indicators for presence or absence of hormones, are still in the anlagen stage; prostate gland is represented by a few knob-like outgrowths from the epithelium of the urogenital sinus, and Mullerian ducts in females are simple undifferentiated straight tubes. Following the removal of testes on day 20 prostate differentiation proceeded uninterruptedly in normal manner and rate until a period later than 100 days; similarly, ovariectomy on day 20 was followed by characteristic differentiation of the simple Mullerian ducts into oviduct, uterus, and lateral vaginal canal up to periods later than the 100 day stage. Regression of the opposite, or heterologous, sex duct proceeded as in unoperated males and females. Since this differentiation of both male and female accessory reproductive structures was, in character and rate of development, the equivalent of that in normal controls, the results suggest two major conclusions: (1) Differentiation of the reproductive system continues up to well defined stages of completeness in the absence of gonads hence such development does not depend upon hormone secretion by the developing gonads, and (2) hormone secretion by the normal untreated gonads can be definitely detected only subsequent to an age of 100 days.

In a comparison of normal development of the opossum and rat, considering such elements as first appearance of a lumen in the seminiferous tubule, canalization of prostate out growths, uterine gland development, first ovarian antrum formation, and still others, the rat of 10 days of age compares favorably in sexual differentiation with the opossum of approximately 110 to 125 days of age. The slower development in the opossum, therefore, permits more definite analysis of hormone effects and development occurring without hormone secretion.

General Summary

In this discussion an attempt has been made to bring to attention some of the considerations required for proper orientation to the problem of whether sex hormones play a role in sexual differentiation. As leading to a clarification of the central problem, and with attempts to avoid so many of the current confusions, it appears advisable to restrict the general term "sex hormones" to that conception which is most appropriate from the historical usage. Sex hormones, therefore, should be limited to the secretions, of a steroidal nature, that are provided through activity of the gonads, designated as androgens and estrogens, and which play a distinct role in the control of morphology and physiology of the accessory organs of reproduction; their natural province of action is the reproductive system, aside from the gonads, and on such characters as plumage or superficial excrescences, and on behavior; some investigators will still question whether these hormones influence the organs which produce them—the gonads themselves. We would thus restrict our application of such terms as sex hormones, gonad hormones, testicular and ovarian hormones, cortical and medullary hormones, and it then becomes a problem to express our notions relative to their time of origin and sphere of operational influence. In turn, we would avoid the inclusion under the term sex hormones of substances produced by adrenals, pituitary, or other sources that might under some conditions exert an influence on sex characters, as well as such other substances possibly produced by chromosomes, or "inductor" substances presumed to express the action of male- and female-determining genes in producing cortex and medulla, and even substances that may possibly operate in a mutually antagonistic manner between cortex and medulla in the final establishment of the gonad. Witschi has designated by special name the hypothetical substances "cortexin" and "medullarin," has spoken of them as "inductor substances," has defined their sphere of action as intragonadal, and not affecting secondary sex characters; he regards these substances as possibly protein-like in nature. Whether the term "inductor" is appropriate for such substances is questioned by some on the basis that inductor actions usually imply a stimulating action whereas Witschi (1940) states

> This interaction manifests itself mainly as a mutual antagonism; effects indicating positive stimulation have not been definitely demonstrated.

The term "inhibitor substances" used by Humphrey (1942) to explain the same phenomena appears less objectionable. Thus

> The inhibitor substance in the Urodele is of the character of a hormone, since it is transported through the blood from testis to ovary in grafted animals, or from male to female in parabiotic twins.

Both Witschi and Humphrey exclude these substances from the sex hormones, and make clear that the sex hormones, produced at later periods in development, are responsible for the secondary sex characters during reproductive life. With this restriction, therefore, what may be said of the role of sex hormones in sex differentiation?

The application of chemical androgens and estrogens during development has induced many modifications, both with respect to the character of gonadal differentiation and in the differentiation of the sex ducts and other accessory sex characters. Some modification of gonadal differentiation after treatment with these chemical hormones has occurred in all groups, with the exception of the mammals, but the modifications have lacked specificity, conformity with the character of hormone, or predictable responses. Furthermore, the many other agents that may induce quite similar responses—in amphibia, temperature changes, overripeness, gonad grafts, non-androgenic or non-estrogenic synthetic steroids; in the chick, muscle, thyroid or other types of chorio-allantoic grafts, handling, chilling of eggs or other manipulations—suggest that where recognized androgens and estrogens have induced modifications the possibility exists that they exercise merely non-specific disturbances of the normal physiological, or genic, mechanisms; they may be no more specific, nor applicable to normal development than is shaking of eggs for the production of rumplessness in fowl (Landauer and Baumann, 1943).

On the duct systems, likewise, responses to androgenic and estrogenic treatments have been so variable and lacking in specificity as to exclude the belief that substances of this nature could be responsible for controlling the normal course of sex differentiation. The responses have been of much general interest in demonstrating the capacity of the ducts to respond to hormones, and frequently to respond to either androgens or estrogens in a non-specific manner. The responses witnessed, therefore, do not lend encouragement to the idea that similar substances operate normally to regulate development of the reproductive system.

The utilization of gonadotropic agents, and early gonadectomies, serves to suggest that actual sex hormone secretion by the gonads begins considerably later in ontogeny than the characteristic disposition of the embryonic duct systems. The available evidence suggests that in the bird sex hormone secretion begins only after hatching, in the rat from birth up to the 10th day, in the guinea pig perhaps slightly later, in the opossum not until an age subsequent to the 100th day of post-natal life. If these suggestions can be admitted to possess any real merit, it would become necessary to exclude gonad hormones as agents in the regulation of sex differentiation of the reproductive system. Finally, the demonstration that gonad removal during the anlagen stage of the reproductive system in the opossum is without perceptible effect on differentiation of the sex ducts (Moore, 1943), and glands (Rubin, 1943), up to day 100, when differentiation is essentially complete, forces us to attend more seriously to the genic sex factor balance to effect differentiation of the reproductive system; the intervention of gonadal secreted hormones to guide these early normal processes is therefore not required.

As a closing consideration relative to the freemartin case, it can be said that a satisfactory interpretation is yet to be given. That the conditions found in this unusual type of development can be explained on the basis of sex hormones as the effective agents is not suggested by any demonstrated modification in mammals. That the testis may be secreting hormones has not been disproved, but all evidence at present available brings it into grave doubt. That the effects of blood intermixture between heterosexual twin pairs are quite unique for ungulates, if not for the bovine species, is suggested. There exists a high degree of similarity in response of the gonadal, but not duct, system to that found in parabiotic urodeles. Responses of the duct system in the freemartin are not yet duplicated by any experimental treatment in mammalia, either under the influence of living tissues, or from treatments with the chemical androgens. It would appear incontrovertible that a humoral substance, transmitted through the blood stream, must be held accountable as the effective agent, but the nature of the substance is not indicated as being of the steroidal sex hormone type; furthermore, that it is a testis secreted substance appears to the writer doubtful, because of the lack of any supporting experimental results. Elsewhere (Moore, 1941) the suggestion has been offered that the chemical differences in the blood stream of genetically determined males and females, possibly from contributions of the cells of the soma tissues in general, rather than the testis specifically, may represent a conditioning agent. In any event, the freemartin still provides the challenge for proper interpretation that it presented more than a quarter-century ago.

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BREEDING *XENOPUS LAEVIS*[1]

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NUMEROUS inquiries have been directed to the Department of Animal Behavior, American Museum of Natural History, within the past year for information concerning the breeding of the South African clawed toad *Xenopus laevis*. The sudden interest in this toad is due mainly to its use as an indicator in the human pregnancy test. (For details of this test see papers by Elkan, 1938, Crew, 1939, and Weisman, Snyder and Coates, 1942a.) An investigation of the possibilities of breeding *Xenopus* in captivity was initiated in the Laboratory of Animal Behavior in 1940. Because of the slow rate at which the young mature, and because of the scarcity of new field material, the problem is far from complete. Nevertheless, because of the many requests, it was thought advisable to report at this time all available information. The following is a progress report of our observations and results, together with some practical advice to those about to undertake the breeding of this toad. A brief review of the literature is included.

The earliest account of the breeding of *Xenopus* which has come to our attention is that of Beddard (1894) who obtained viable eggs in the gardens of the London Zoological Society in 1894. A few years later Bles (1901) obtained similar results, and in 1906 Bles published a detailed report of a method by which *Xenopus* could be bred in a small laboratory aquarium. The major points established by Bles (1906) were: (1) The *Xenopus* should be allowed to hibernate over the winter. As a prerequisite for successful hibernation, the toads should have had adequate light, heat and food the previous summer. (2) In the spring, the temperature of the aquarium should be raised to 22° C. (3) Water should be drawn off daily, allowed to cool, and then run back slowly in such a manner as to simulate rain. (4) When the eggs hatch, food in the form of concentrated flagellate cultures must be added daily. Bles raised his tadpoles through metamorphosis, and raised at least one male to maturity in two years.

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[1] This study was supported by a grant from the Committee for Research in Problems of Sex, National Research Council.

In addition to these successful endeavors to raise *Xenopus* in captivity a number of aquarists (Kotthaus, 1933, Senfft, 1939, and Hogjaard, 1940) have reported breeding the African clawed toads and rearing the young. It is evident from the above reports that if optimal environmental conditions are established, *Xenopus* will occasionally breed in captivity. However, the methods used are neither dependable nor practical. If optimal conditions are not created the female toads will not ovulate in captivity (Shapiro, 1936a, 1936b) and this fact is a major premise for their use in the pregnancy test.

Hogben, Charles and Slome (1931) were the first to demonstrate that a gonadotropic hormone would cause *Xenopus* females to ovulate. Shapiro, using a human pregnancy urine extract (1936a) and an anterior pituitary extract (1936b) obtained fertile eggs, and reared some tadpoles, but he was unable to bring them through metamorphosis. Landgrebe and Purser (1941) reported briefly a method of raising *Xenopus* using gonadotropic hormone, but details are lacking, and their method of feeding the tadpoles is cumbersome.

BREEDING METHODS

Sexing the Adults. While it is difficult to sex the immature toads, the sex of the adults can be readily determined. The three cloacal lips of the female are large and are easily distinguished, while the homologous structures on the male are small and are barely visible. Secondly, black nuptial excrescences are usually present on the ventral surfaces of the forelimbs of the males. These pads have been pictured and described in detail by Berk (1939).

Maintaining the Adults. We have found that an adult pair will get along very well in a 10 to 15 gallon aquarium, or 4 to 6 pairs in a 50 gallon tank. If care is taken not to put more food in the tanks than the toads will consume, the water need not be changed more than once a month or even less frequently. To minimize pollution of the water, we have placed aerators in our tanks. While this is a convenience, it is not absolutely necessary. Finely minced beef muscle or liver fed daily is a satisfactory diet. In addition we have found that a coarse grade of dehydrated tropical fish food (consisting of oatmeal, lettuce, spinach, dried shrimp and liver) is a convenient and satisfactory alternative. We do not recommend a diet consisting wholly of the dehydrated food.

The toads can stand considerable and even abrupt changes in temperature, but it is probably best to keep them around 70° C. They seem to thrive under light conditions varying from total darkness (Bellerby, 1938) to bright sunlight. Here again a moderately lighted room is probably most desirable. Landgrebe (1939) studied the effects of food and crowding on the maintenance of reproductive activity in *Xenopus*. He recommends feeding the toads with liver at least once a week, and either keeping the toads in running water, or else at a maximum concentration of one 50 gr. toad per liter of water. Some investigators (Elkan, 1938, Crew, 1939) claim that the water must be changed after each feeding. We have not found this to be necessary. Only large quantities of excess food pollute the water, and this can easily be avoided. We have received inquiries concerning the sudden deaths of large numbers of toads during the summer months, and we too experienced this difficulty on one occasion. Changing the water and sterilizing the tanks did not help, but when the remaining stock was removed to a dark cool room, no more deaths occurred. On the other hand, we have been able to keep part of our stock healthful and in good reproductive condition in a sunlit greenhouse at 25° C., where the temperature sometimes rises to 35° C. Other than the one occasion mentioned above, deaths have been very infrequent.

Induction of Spawning by Hormone Treatment. To induce spawning, the males and females were injected intraperitoneally with a sheep anterior pituitary extract known as 3819-preloban.[2] The doses used and the results obtained are recorded in Table I. If no eggs were obtained with one dose a second injection was given 24 hours later, and if no eggs resulted, a third injection was given 48 hours after the first treatment. Toads that did not respond after the third treatment were not given any more hormone, and are not listed in the table. One mg of preloban is approximately equal to 1.2 rat units.

From Table I it is evident that a single dose of from 4 mg to 8 mg caused the female to ovulate too rapidly resulting in large complements of infertile eggs. (There is also a possibility that the infertility of the eggs was caused by too strong an injection into the male, but this is unlikely.) It is also apparent that a dose of 2 mg was slightly subminimal for most females, and that when this amount of hormone was injected 24 hours after the first treatment many pairs yielded large quantities of fertile eggs. A second dose of 4 mg for the females was also satisfactory. Finally it is evident that two successive injections of 2 mg each were sufficient for the male. It is probable that many of the males did not require any hormone treatment to induce breeding.

Due to the scarcity of adult toads, other gonadotropic hormones have not yet been tested. The studies of Weisman *et al.* (1941, 1942b) show that the dose required to cause a female to ovulate varies considerably for each hormone used. From these data a slightly subminimal dose for each hormone which these authors used can be calculated, and it is reasonable to predict that for the female, a subminimal dose followed 24 hours later by twice that amount should be satisfactory. Likewise, two successive subminimal doses should be satisfactory for the male.

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[2] The anterior pituitary extract was supplied by the Winthrop Chemical Co., New York.

The injected pair should be placed in a 15 gallon aquarium. It is advisable to place a water soaked log on the bottom of the tank, since the female attempts to deposit the somewhat adhesive eggs on solid objects in the water. From the spawning of male 9 and female 10 samples were taken of the loose eggs, and also of eggs adhering to the log. These counts showed that only 10 per cent. of the loose eggs were fertile while 75 per cent. of the adhesive eggs were fertile. While in other spawnings the percentage of fertile loose eggs was estimated to be much higher, the use of the log still seems desirable.

TABLE I

INJECTIONS OF SHEEP ANTERIOR PITUITARY EXTRACT—PRELOBAN

Pair	Date of first injection	Size of first injection in mg	Size of second injection in mg (24 hours later)	Size of third injection in mg (24 hours later)	Results Within 24 hours after last injection
♂ 23 ♀ 23	10/31/40	8[*] 4			Large complement of eggs—none fertile
♂ 24 ♀ 31	11/3/40	8 8			Large complement of eggs—none fertile
♂ 5 ♀ 6	12/2/40	3 2	3 2	3 2	Large complement of eggs—many fertile
♂ 13 ♀ 15	2/18/41	2 2	.. 2	2 4	Large complement of eggs—app. 75 per cent. fertile
♂ 7 ♀ 8	3/14/41	2 2	2 2		Large complement of eggs—app. 75 per cent. fertile
♂ 11 ♀ 12	3/28/41	2 2	2 2		Large complement of eggs—few fertile
♂ 18 ♀ 19	5/12/41	2 2	2 2		Small complement of eggs—many fertile
♂ 33 ♀ 20	3/4/43	2 2			Small complement of eggs—many fertile
♂ 1 ♀ 14	4/1/43	2 2	2 4		Large complement of eggs—many fertile
♂ 12 ♀ 35	4/1/43	2 2	2 4		Large complement of eggs—many fertile
♂ 9[†] ♀ 10	5/19/43	2 2	2 2	2 2	Large complement of eggs—app. 10 per cent. fertile

[*] 1 mg preloban is equal to approximately 1.2 rat units.
[†] Pair reared in laboratory.

The adults should be removed from the tank as soon as possible after the termination of the oviposition to prevent their damaging the eggs.

Rearing the Tadpoles. After the adults have been removed and the eggs have been checked for developing embryos, an ordinary aquarium aerator should be placed in the tank. One or two lettuce leaves previously boiled and cooled should now be added to the water. No attempt should be made to remove undeveloping eggs, since the decaying eggs and decaying lettuce will form the culture medium for bacteria and other microorganisms upon which the tadpoles will soon feed. The outer leaves of the lettuce (generally discarded by the vegetable dealers) are satisfactory. They should be brought to boil in a little water, and may be stored in a refrigerator until needed (Hyman, 1941).

The tadpole aquarium should be checked once every other day. If the lettuce is mostly disintegrated more should be added. If too much lettuce is added the water will begin to develop a distinctly foul odor and the tadpoles will start floating at the surface. When this condition is noticed, the aeration should be increased and no more lettuce should be added until the foul odor disappears. After a few weeks considerable debris will accumulate in the tank, but we have not found this to be the least bit harmful, and it should not be removed. We have observed that *Xenopus* tadpoles are rather sensitive to handling. Consequently such procedures as cleaning the tanks should be avoided if possible. If the proper aeration is maintained and not too much lettuce is added at one time, it is possible to bring all of the tadpoles through metamorphosis without ever changing the water.

The tadpole aquarium may be placed in any situation varying from total darkness to bright sunlight. However, too much direct sunlight will cause the water to turn green, and this will make inspection difficult.

If it is desired to rear the tadpoles rapidly, they should be thinned out. This is done by filling other aquaria with water and adding some boiled lettuce, at least 3 or 4 days before using. Fresh tap water should be avoided. The embryos or young tadpoles are delicate and should be handled gently. If about 10 to 20 tadpoles are placed in a 15 gallon aquarium, the first tadpoles should begin to metamorphose in one month, and the slowest growing tadpoles should start metamorphosing within two months.

If it is desirable to prevent the tadpoles from metamorphosing rapidly (as for demonstration purposes), they should be crowded (100–200 in a 15 gallon tank). When this is done the fastest growing tadpoles will metamorphose in one to two months, while the slowest growers will remain in the larval stage for 4 to 6 months or more.

Metamorphosis. As contrasted with our local Anura, this stage in *Xenopus* does not present any difficult problems. A variety of small live foods are satisfactory for the baby toads such as tubifex worms, Naid oligochaetes, white worms (*Enchytrae*) and Chironomus larvae. (See Hyman, 1941, for methods of culturing some of these forms.) The oligochaetes were sometimes grown in the water along with the tadpoles.

As the tadpoles complete their metamorphosis, they may be removed to a new tank. After a month or two, live food may be dispensed with, but even before this if live food is not available, a medium grade tropical fish food can be used. This should be sprinkled into the water directly above the little toads to attract their attention. Liver cut into very small pieces should also be used.

The F_1 Generation. In 6 to 8 months some of the males born in our laboratory from wild stock became mature and were successfully mated to our wild females. These males were less than half the size of a full grown adult. The females born in captivity appear to be less likely to reproduce. Although some of the females are over 2½ years old and are almost full grown, only one of them has bred thus far. This particular female was approximately 2 years old when hormone treatment began. It is not clear why the F_1 females are reluctant to breed. They might still be too young. The conditions under which they were raised might not be satisfactory. Treating the animals with gonadotropic hormone before they were fully mature might have resulted in an inhibition of the ovaries or an anti-hormone effect.

From the single F_1 spawning an F_2 generation is being reared and there is some possibility of developing a strain of *Xenopus* that will readily breed in captivity.

Concluding Remarks

The question has been asked many times why our local frogs and toads can not be used for pregnancy diagnosis. The comparison of *Xenopus* with local American Anura as given by Weisman, Snyder and Coats (1942b) is not satisfactory. These authors state that "The Xenopus frog differs from the common variety of American frogs in that it constantly ovulates and accordingly carries the ova in its abdomen. The eggs are extruded in natural life only upon stimulation by the male of the species." There is no reason to believe that these toads constantly ovulate. Similar to American Anura, *Xenopus* has a definite breeding season (from July to September—African spring Shapiro, 1936a, Berk, 1938), the only difference being that the *Xenopus* female apparently lays part of the eggs each night for a number of successive nights (Bles, 1906). That the clasping male stimulates the female to ovulate has been hypothesized many times for Anura (Hartman, 1939, quoting Nussbaum, 1895, 1897, Bragg, 1941). However, the evidence for this concept is weak. On the other hand, there is some evidence that in *Rana* and *Xenopus* (Noble and Aronson, 1942, Shapiro, 1936c) the male will not clasp the female until she is first stimulated to ovulate, apparently by environmental changes in rainfall and temperature (Berk, 1938). If the environmental conditions are satisfactory, there is reason to believe that female *Xenopus* would extrude eggs even if isolated from males. It is possible that the call of the males might act as an auditory stimulus, or that the sight of the male might act as a visual stimulus, and that these stimuli might be two out of many which cause a female to ovulate, but this has not as yet been demonstrated. In our aquaria, the presence of calling males never caused any female to ovulate.

The major differences between *Xenopus* and most other Anura relative to the pregnancy test is the extreme sensitivity of the ripe ovaries of the clawed toads to various mammalian gonadotropic products as compared with the slight sensitivity of other Anura to these same preparations. Secondly, it appears that in *Xenopus,* all the eggs that are ovulated pass promptly down the oviducts and are extruded even though they be few in number. In many other Anura particularly *Rana,* the ovulated eggs accumulate in the lower part of the oviduct (uterus). Whether such eggs are extruded, oviposited (Noble and Aronson, 1942), or retained indefinitely in the uterus depends upon such factors as the number of eggs in the uterus, rate of ovulation, the clasp of the male, temperature, etc.

While it might never become economcially practicable to raise *Xenopus* in captivity either for the pregnancy test, for food, or for any other purposes, if these toads can be bred with reasonable success, the value of *Xenopus* as a laboratory animal will be greatly enhanced. For those not well acquainted with *Xenopus,* the following virtues of this toad as an experimental animal as compared with our local Anura are listed: (1) Live food (or forced feeding) which most other Anura require, is not needed. (2) Any kind of tank or container of water is satisfactory to keep the animals in good health. (3) If necessary, the water need be changed only a few times a year, and feeding may be reduced to once a week. (4) While metamorphosis presents a difficult hazard to the breeder of most Anura it offers no difficulty whatsoever for *Xenopus.* The recently metamorphosed toads can be fed just as easily as the adults.

It is hoped that this report will answer a few of the questions concerning the breeding of *Xenopus,* and will act as a guide to those who may be contemplating such a project.

ADDENDA

(1) A paper on the breeding of *Xenopus* has just been received. (Paul Gasche—1943. *Rev. Suisse de Zool.*, 50: 262–269). The method of raising the tadpoles which this author suggests does not appear to be very appropriate. On the other hand Gasche states that with intensive feeding of liver, and by changing the water on alternate days, mature females were reared in eight months.

(2) Since this report was submitted for publication, four additonal laboratory reared females were induced to ovulate. Each female received a daily injection of 2 mg of preloban for four consecutive days.

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GENETICS OF BODY SIZE AND RELATED CHARACTERS

I. Selecting Small and Large Races of the Laboratory Mouse

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Introduction

An experiment was started in 1939 whose objective was to produce by selections from one original population both an extremely small and an extremely large-bodied race of the laboratory house mouse. Such races did not exist either in the rat or mouse, though Goodale had very successfully increased mouse weights by selection, and considerable size differences are found between closely allied species in mice (*Mus bactrianus* and *M. musculus*), and in guinea pigs, and between some breeds in rabbits.

This work was undertaken in the belief that stocks showing the widest possible contrast in body size, once developed in some common small experimental mammal, might prove as useful aids in genetic studies of typical quantitative characters, as have the stocks possessing diverse color combinations for the study of qualitative characters. They could be used advantageously for demonstrations and for much-needed more exact investigations on inheritance of differences in size, in growth rates and in hybrid vigor. Meanwhile the trends of the selections themselves throw some light on the nature of size inheritance, and may aid in reinterpreting some older selection experiments.

It will be noted also (in Part II) that, clustering around body size as the central character, are found associated intimately a whole system of other correlated or satellite characters of not a little general biological interest, involving as they do such basic problems as the physiology of mammalian reproduction, fertility (litter size), behavior (activity and wildness), growth and relative growth (ratio of appendage length to body measurements).

The research was done with the laboratory mouse, but the findings quite evidently have a more general significance, for they apply, in some respects at least, as has been shown (MacArthur, 1942), to man and to other mammals, both domesticated and wild. And, as it turns out, the production of these races parallels in a number of ways raciation processes occurring in nature.

The results certainly illustrate the great efficacy of selection as an agent for the modification of size (and the various characters that follow in its wake) and are likely, of course, to have some practical bearings in the way of offering suggestions or giving directions for breeding more economical, larger and more prolific farm animals.

PLAN OF THE EXPERIMENT

Preparation of the Foundation Stocks. The population from which the selections began was derived ultimately from several fixed inbred strains of laboratory mice, commonly used in many laboratories for demonstrations of color inheritance. Seven strains in all were interbred in four separate crosses, and their hybrids were again interbred at random to produce a large "F_2" population, the foundation stock.

The strains used were the familiar long-inbred "dilute brown" (*dba*) and "silver chocolate" (*sv ba*) from the Jackson Memorial Laboratory; "black and tan" (a^t), and pink-eyed, short-eared "dilute brown" (ps^edba) from the University of Michigan; and our own stocks of "albino" (*c*), "cinnamon spotted" (*bs*), and "agouti."

These strains were chosen principally because they were average and undistinguished in body size, carried no unusual mutant size genes (for dwarfness, etc.), and were free from abnormal factors (tailless, hairless, lethal yellow, high cancer, etc.). They were hybridized to increase the field of variation, by bringing together into the melting pot as wide an assortment as possible both of the more normal qualitative Mendelian factors and also, and especially, of the size genes or modifiers controlling quantitative differences in growth rates and body sizes.

Four different matings produced young as follows:

Parents		*F_1 young*
female	male	
black and tan	cinnamon spotted	9
albino	dilute brown	3
silver chocolate	ps^{e}dba	6
black and tan	agouti	8

The 26 F_1 young were allowed to interbreed uncontrolled in a single large cage. They produced a large F_2 population ultimately numbering several hundred mice.

Separation of Reserve and Experimental Stocks. The month-old young were removed from the F_1 breeding cage and isolated by sexes in two large cages. These were later divided at random into an experimental portion from which the special size selections were made, and a remnant reserved as control. The larger control lot is being maintained as a single group by mass breeding without deliberate selection.

The experimental group withdrawn consisted of equal numbers of females and males. As they matured 30 were mated without regard to size, each pair in its own small cage. Their first and second litters, totaling 101 males and 117 females, were reared to at least 60 days. These "F_3" litters collectively constitute Generation O of the selection experiment.

Establishment of Small (S) and Large (L) Lines. The young of each litter were weighed collectively at birth, and later sexed, phenotyped and ear-marked and weighed again at least at 30 and 60 days. The weight approximately doubles between 30 and 120 days, but at two months of age the growth curve has so flattened out that the 60-day weight affords a reliable indicator of the final body weight.

Each litter was then roughly classified as either "small" or "large," judging from the average of weights of its component individuals. Small mice and especially those from half of the litters with smaller-than-average 60-day weights became the progenitors of the small race. The successive generations selected to maintain and build up the small line are recorded in this paper as S_1, S_2, . . . S_8. The large line (L) similarly began with the large individuals taken from the litters of higher-than-average 60-day weights. The small and large lines have since remained isolated and self-sufficient. No genes have been exchanged between them, since they were first separated, and no new blood has been introduced from outside into either line.

That the preliminary mixing in the melting pot had been reasonably efficient (though of course far from complete) is shown by the fact that all the different qualitative genes represented in the original strains were recognized, at least in early generations, in both the S and L lines, and they still remain in the remnant "control" stock cage.

CARE OF THE STOCKS

To reduce environmental inequalities to a minimum all the mice were kept continuously in the same air-conditioned room-temperature laboratory murarium, fed the same foods (wheat grain, fox chow, lettuce, etc.) and the cages were rotated in position from time to time. Seasonal changes in daylight, artificial lighting, humidity and temperature were shared by all groups alike. No artificial stimulation, by feeding of vitamin concentrates, like wheat germs, or by hormone treatments, was employed on any stocks. The changes produced by selection in the body sizes and other characters are thus unquestionably, for the most part, of a permanent and hereditary, and not of a temporary and environmental nature.

SYSTEM OF MATING IN THE S AND L LINES

The small and large selection lines are maintained by the mating each generation of approximately 5–10 males and 20–35 females. These are always bred as pedigreed pairs, never en masse. In general each male is mated at one time or another with 4 to 8 or 10 females in his breeding cage, from which each pregnant female is removed to her special numbered cage (*e.g.*, 1). Here her young are born and reared until weaned; the young females are left with the mother, while the young males are transferred to their correspondingly numbered cage (1 a). The mother may then be remated with the same male, or (if the first litter was not promising at the 30-day weighing) with a different male, or even discarded.

In general the attempt is made to secure about 10 progeny from each pairing from which to judge the genetic worth of the family. For this purpose one litter usually suffices in our present L_8 stock, but two successive litters are required in the S_8 stock, owing to the small average number of young born in each litter (part II).

The S and L stocks are maintained with little continuous inbreeding and no deliberate line breeding. No separate "sublines" or "families" are established in either stock. The S stock, for instance, contitutes at any generation one interbreeding population, in which new combinations of size genes are brought together by diverse pairings, and the best combinations are detected, if possible, and preserved by selection. On the other hand, inbreeding is not avoided, for sibs and other relatives are often mated. The intention is to mate assortatively, like with like, more or less irrespective of relationship, and also without attempting to fix (make homozygous) any gene pairs, or, if they chance to be fixed, to keep them so.

Since each breeding population is relatively small, consisting as it does of what is something like a "5–10 sire herd," closed to outside blood, one would expect a slow loss of heterozygosis, and loss or fixation each generation of some size genes and some qualitative genes. From Wright's formula the rate of reduction of the remaining heterozygosis may be roughly estimated as $\frac{1}{8M} + \frac{1}{8F}$, or something like 1 to 3 per cent, per generation. This should gradually cause the lines both to change gradually by "drift" and to become more uniform, even independently of selection.

CRITERIA OF SELECTION

In each of the lines the "best" 5–10 males and a select group of some 20–35 females have to be picked as breeders to produce the following generation. These are commonly chosen from about 60–120 individuals of each sex, in each line. In general we wish to identify, save and breed the group that would represent a deviation from the average of about $1.3-1.6\,\sigma$ for males, and $0.7-1.0\,\sigma$ for females.

In the L line, for example, the object is to accumulate and concentrate all possible different and possibly interacting large size genes by the plus selection. The mice most likely to possess such genes are chosen on the basis of:

(1) *The progeny test.* The principle of the progeny test is given in the familiar quotation: "By their fruits ye shall know them." Ten or twelve young afford a fair practical sampling of the genotype of the parents. Sixty-day weight data are at once transferred from cards to summaries, tabulated as a frequency table, so that the body size of each sibship and individual may be compared with the frequency distribution of the preceding and current generations. The already highly selected and extreme parental pairs are not usually even equalled by their progeny. Running progeny tests discover which few of the select pairs actually do transmit exceptional size. If all or nearly all the progeny excel the average of the preceding generation in 60-day weights the parents must have formed a favorable combination as partners.

(2) *Individual performance.* Those individuals which on their own records of growth in size appear to represent a promising combination of the various size genes segregating and assorting within a sibship of 10 or 12

are favored tentatively because they have exceeded their sibs.

(3) The selection is thus based primarily on the progeny tests and individual phenotypes, with a further effort to keep the basis of selection broad by choosing for breeding at least one female from each even moderately promising family, rather than achieving a more spectacular but less lasting success at a sacrifice of continued variability.

Selection between breeding pairs proceeds actively within a given generation. Progeny distinctly below standard at 30 or 60 days are discarded, and the parents may also be culled or mated to different partners. The pairs which have distinguished and proven themselves by producing a litter especially promising at 30 or 60 days are again mated together or each with other promising mates. These additional litters are evidently particularly important features of successful progress in selections guided by progeny tests. (An incidental result of this practise is that the mean of the population is artificially shifted and the distribution skewed toward the small end of the curve in the S stock and toward the large end in the L stock.)

A certain amount of reproductive selection of course occurs each generation against barren matings and shy or late breeding individuals. Extremely obese large mice or runty "dwarf" small ones have usually proven sterile or practically so. This is fortunate, since we did not aspire to produce freak types. On the whole the few monstrous or "abnormal" or sickly mice that appear present no major problem, since these seem to be practically self-eliminating.

A further point should be mentioned. The largest stock females may produce as many as 16 or 18 living young in one litter. Since so many young might be handicapped in their growth before weaning the number of young retained in such litters has (since the 8th generations) been restricted to 10.

PROGRESS OF THE PLUS AND MINUS SELECTIONS

Gradual and Progressive Divergence of the Small and Large Races. Selection, especially when it follows recent extensive hybridization, is a powerful agency for change in organisms. There were special reasons for expecting success with this material. Recombination of factors in mouse chromosomes is known to be comparatively high and to provide a continual supply of new variability by crossing-over (Crew and Koller). Goodale found it rather easy to increase size in an albino stock.

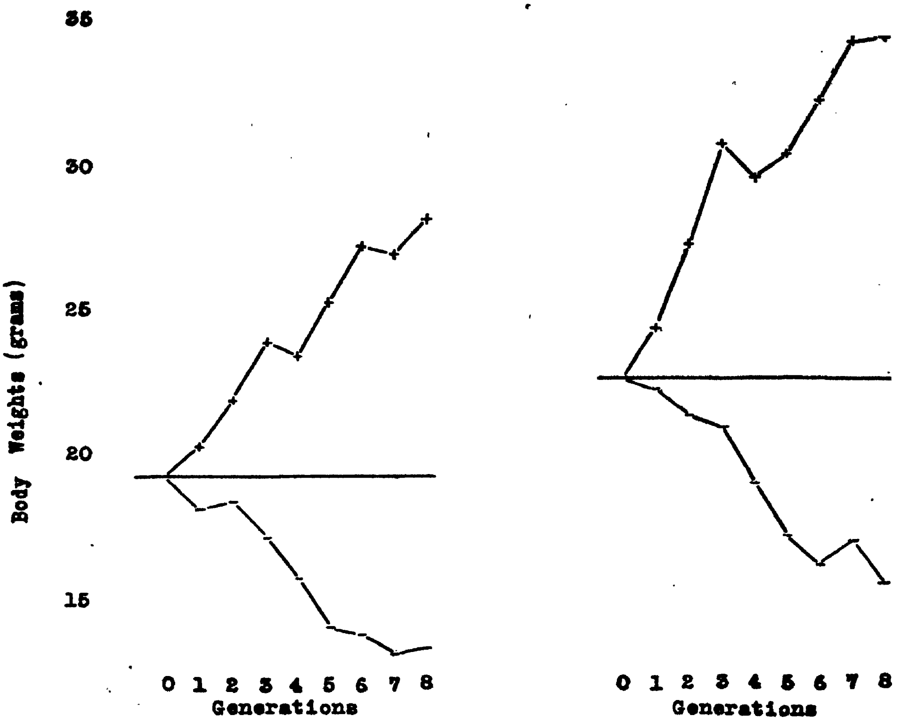

FIG. 1. Divergence of mean 60-day weights of females (left) and males (right) during 8 generations of plus selection (— + — +) and minus selection (— – — –).

Actually the mice used proved to be so plastic and variable that they are being rapidly "made over to size" by the plus and minus selections. Regression is generally positive, large parents typically producing large progeny, and small parents small. As a general rule each succeeding generation sees the small and large races diverging more and more in their average 60-day weights (Fig. 1), and still more in their final weights. Moreover, there is every prospect of continued, but undoubtedly slower, divergence with further selection.

The size difference between races is already present and distinct at birth and steadily widens with growth, at first quickly and then slowly, in the postnatal period. When neutralized as to sex the difference, 26 per cent. (1.18 *vs.* 1.49 gms.) in new-born, birth-fed young, increases to 68 per cent. (11.74 *vs.* 19.76 gms.) at 30 days, and 108 per cent. (14.94 *vs.* 31.11 gms.) at 60 days, and is still greater at advanced ages, especially in females. Growth is more rapid and more prolonged in the large race.

TABLE 1

Least, Average and Greatest 60-Day Weights of Male and Female Mice Through the First Eight Generations of Selection to Decrease Size (Small Race, Left) and to Increase Size (Large Race, Right). The Few Recessive-Type "Runts" Excluded. Each Range and Average Based on 59–115 Individuals.

Generation	Small line						Large line					
	Males			Females			Males			Females		
0	18.5	23.2	31.9	13.9	19.5	26.9	18.5	23.2	31.9	13.9	19.5	26.9
1	16.6	22.9	28.6	12.9	18.6	23.5	18.2	24.6	32.3	15.1	20.8	27.8
2	15.5	21.9	27.0	13.3	18.8	21.9	20.1	27.9	36.3	14.6	22.2	30.2
3	14.7	21.4	29.5	13.0	17.6	23.0	21.1	31.2	43.0	18.6	24.4	38.4
4	12.7	19.5	29.0	10.7	16.1	22.8	23.4	30.0	36.9	18.2	23.9	36.4
5	12.6	17.9	22.8	10.8	15.2	19.7	22.9	30.9	41.4	19.6	25.6	36.8
6	14.3	18.1	24.4	11.9	15.3	21.0	24.6	32.7	41.6	20.6	27.6	36.2
7	10.4	17.4	22.0	9.7	13.9	18.0	28.2	34.7	42.6	19.8	27.5	37.3
8	10.8	16.0	20.6	10.6	13.8	22.6	27.5	33.7	41.0	18.7	28.4	38.2

For a period during the fifth to the seventh generations a small number of runts (11 out of 212 males and 15 of 239 females) segregated as recessives from the small line only. Somatically they resemble the dwarf mutant. As their growth practically ceases at about 7 to 9 grams, they form a separate group of distinctly smaller size with short ears; they are of low vitality and apparently sterile. Selection against pairs producing them has since all but eradicated this type.

Quantitatively the trends of the changes induced by selection consist in a general, but not entirely steady, decrease of the means and of both extreme weights in the small race, and their increase in the large race (Table 1).

In Fig. 2 are shown the frequency distributions of male 60-day weights in the unselected population, and in the small and large lines after four, and again after eight generations of selection. It was noted above that the distributions are likely to be skewed arbitrarily by rematings. Large sibships of similar sibs tend to make the numerous lesser peaks on the curves.

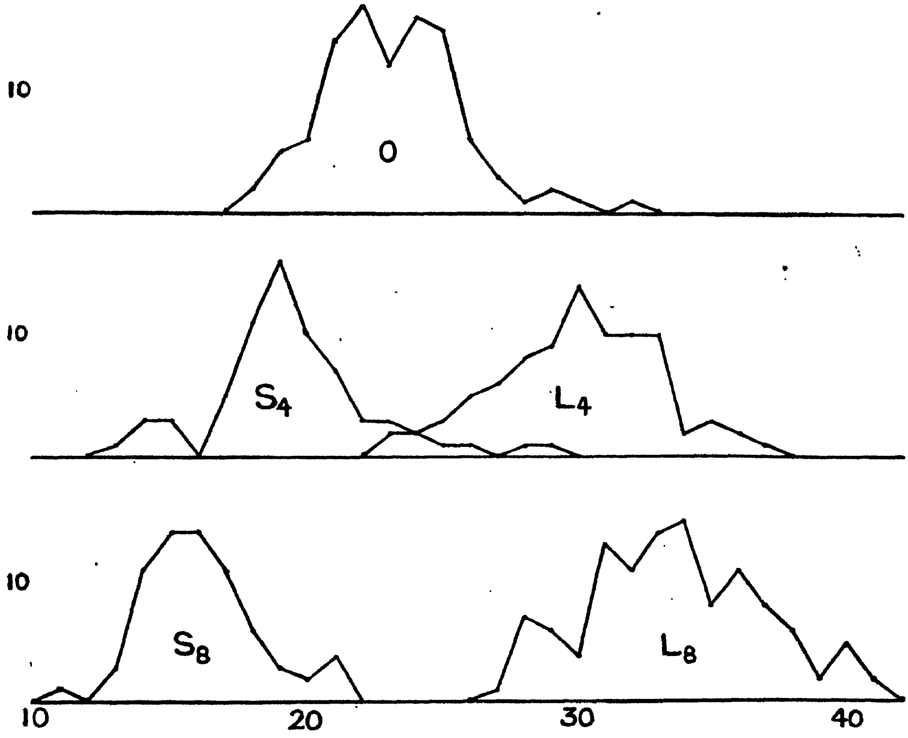

FIG. 2. Frequency distributions of 60-day weights of male house mice in the foundation stock sample (0, above), after 4 generations of selection (middle row, S_4 left, L_4 right), and after 8 generations of selection (lower row, S_8 left, L_8 right).

After the sixth generation, overlapping of the S and L curves (each based on samples of less than 116 mice) became rare and has now practically ceased. The least mice of the large race are larger than the greatest of the small race.

TABLE 2

Differences Between Average 60-Day Weights (Grams) of the Large and Small Races of Mice Resulting from Eight Successive Generations of Plus and Minus Selection. The Gap Between the Races has Widened Steadily but by Lessening Amounts as the Experiment Proceeds. For Males, for Instance, the Divergence per Generation Averaged 2.7 Grams in Generations 1–4; 1.8 Grams in Generations 5–8; and Less Than 1 Gram in the Latest Generations, 9–12.

Generation	Differences between races Females	Differences between races Males
0	0	0
1	2.25	1.69
2	3.31	5.99
3	6.73	9.76
4	7.76	10.51
5	10.44	13.07
6	12.30	14.78
7	13.95	17.44
8	14.79	17.81

There are, of course, far smaller mice in the small race (S_8) and far larger ones in the large race (L_8) than were found among the approximately equal numbers reared in the initial generation before selection began.

After 8 generations of selection the average difference between the races clearly exceeds the mean absolute weight of the small race (Table 2). Small race males then averaged 16 grams; the large race males were 17.8 grams heavier at the same age and generation. The small females had a mean weight of 13.8 grams, while large race females exceeded this mark by 14.8 grams.

Data and calculations condensed in Table 3 show the significance of the size differences brought about by selection and also the promise of continued success with

TABLE 3

Sizes (60-Day Total Weights in Grams) of Males and Females from the Unselected Foundation Stock (Gen. O), and from the Small and Large Races After Four and Eight Generations of Minus or Plus Selection. The Differences Between Mean Weights of S_8 and L_8 Mice Exceed 28 Standard Errors.

Generation	Males Mean weight	Males Standard deviation	Males Coefficient of variability	Females Mean weight	Females Standard deviation	Females Coefficient of variability
L_8	33.71 ± 0.31	3.31	9.81	28.43 ± 0.39	3.83	13.48
L_4	30.00 ± 0.30	2.76	9.20	23.87 ± 0.34	3.52	14.72
O	23.16 ± 0.26	2.56	11.01	19.51 ± 0.25	2.65	13.52
S_4	19.49 ± 0.32	2.62	13.44	16.11 ± 0.26	2.21	13.72
S_8	16.14 ± 0.25	2.11	13.07	13.80 ± 0.19	1.83	13.25

further selection. Over the eight generations there has been no very definite diminution of total variability in 60-day weights, as measured by the coefficients of variability. But recent gains (and losses) in weight by selection appear to be falling off slowly (see data in legend of Table 2).

INTERPRETATION OF THE RESULTS OF THE SELECTIONS

It is desirable to establish that at least approximately equal selection efforts were made to reduce size in the S race by accumulating minus size genes, and to increase size in the L race by discovering and saving large-size genes. During the eight generations of breeding the actual selections in the small race were based mainly on data obtained from 166 different fertile pairings and from 230 litters of progeny. The selections meanwhile made in the large race were based on 144 different successful pairings and on 213 litters of young. There were thus in fact more pairings made, more cages occupied and more litters produced and used in the "small" than in the "large" selections. But it is only fair to note, on the other side, that, owing to the gradual, and at first unsuspected, divergence of litter sizes (number of young per litter) in the two races (see part II) the actual number of young produced and reared to the final weighing ages was greater in the large race than in the small. In all, 1,099 mice of the small race and 1,504 of the large race were weighed in at 60 days. These were divided about equally between the sexes (1,291 males to 1,312 females).

Selections were based primarily on litter or sib averages plus uniformity, secondarily on individual phenotypes. As seen above, there was a slightly better chance of picking exceptional litters in the small race, exceptional individuals in the large. Selection was rather more intense between litters in small, within litters in large. Whether these factors approximately balance we do not know. At any rate it was the intention to try equally hard throughout the experiment to change the sizes in both sexes and in both directions.

Plus selection more effective than minus selection. Though about the same efforts were expended to raise as to lower body size, it is clear that divergence from the original stock was not equally rapid or marked in the two directions, providing the divergence is measured in absolute grams of body weight gained or lost during the selections (Fig. 1 and Table 4).

It is apparent from these data (1) that the large race has increased considerably more and faster by plus selection than the small race has decreased in size by minus selection, and (2) that the size of the male mice has changed more than the size of females in both plus and minus directions. Thus the males gained 10.55 grams and lost 7.02 grams, while the females gained only 8.92 grams and lost but 5.71 grams.

TABLE 4

AVERAGE 60-DAY WEIGHTS IN GRAMS OF MALE AND FEMALE MICE OF THE FOUNDATION STOCK (O) AND AFTER EIGHT GENERATIONS OF PLUS SELECTION IN THE LARGE RACE (L_8) AND MINUS SELECTION IN THE SMALL RACE (S_8). GAINS AND LOSSES EXPRESSED IN ABSOLUTE GRAMS, IN DIFFERENCE OF LOGARITHMS OF WEIGHTS, AND IN PERCENTAGES ($O > S_8$, $L_8 > O$).

	Males				Females			
		Difference in				Difference in		
	Weight	Grams	Logs	Per cent.	Weight	Grams	Logs	Per cent.
Large race (L_8)	33.71				28.43			
		+ 10.55	.1629	45.6		+ 8.92	.1633	45.7
Foundation (O)	23.16				19.51			
		− 7.02	.1569	43.5		− 5.71	.1503	41.4
Small race (S_8)	16.14				13.80			

Inadequacy of the current theory of size inheritance. The orthodox theory, illustrated in most genetics texts by inheritance of length of corn ears or tobacco corolla tubes, implies that plus and minus size genes or modifiers exert effects, which may be stated as precise quantities, and each of the multiple factors controlling size is considered to add to or subtract from the body weight some constant and definite amount measurable in ordinary units such as grams. Our results are not in accord with this arithmetic view. The data cited count rather heavily against it, and in fact raise considerable doubt as to the perfect symmetry of the "normal" curve of distribution of size differences.

The geometric theory of size gene interaction. On the other hand, the gains by plus selection and the losses by minus selection become nearly, though not quite, equal when the changes in either direction are measured and expressed in the form of difference of logarithms or in percentages (Table 4).

When similarly expressed the average male 60-day weight exceeded that of females by 18.7 per cent. in the unselected stock, and by substantially the same percentage in both the small race (17.0 per cent.) and the large race (18.6 per cent.). Calculated as percentages the gains or losses are practically balanced and equal in both sexes, and the sexual dimorphism in size remains at least approximately constant throughout the experiment. Here again the effects of the selections on growth rates and sizes are most simply described by transforming the data to a logarithmic or percentage scale.

These basic data clearly suggest that the influence of a size gene or modifier is not a constant quantity definable in absolute amount, but rather that the effect of such a size gene or modifier increases as body size increases and lessens as body size diminishes. In other words, the characteristic and essential effect of a size gene is that it depends on some standard of reference and is relative, being proportional to body size as potentially determined by the remainder of the genotype. Size genes appear to multiply rather than summate each other's effects. This is the same geometric concept of size gene action and interaction in inheritance that was arrived at by previous studies of fruit sizes in hybrids from crosses of large and small-fruited varieties of tomatoes (MacArthur, 1941). The fruit sizes from dozens of crosses of different types *fit too closely and too regularly to the geometric mean to* be plausibly confused, as Mather contends, by phenomena of dominance and epistasis.

On this geometric view selection effects are comparable to growth changes. At least over a limited series of generations, while plus or minus genes are abundant and readily accumulated and concentrated, the rate of change by selection may be likened to rate of growth of individuals or populations in time, and expressed as an exponential increase of a capital by the compound interest rule. Thus the rate of change by selections is most conveniently and adequately expressed, not by the absolute number of grams gained or lost, but by the percentage of gain or loss per generation, the increase or decrease being preferably compounded (at a diminishing rate, of course, as variability declines) each generation.

SUMMARY

A large population was made up by hybridizations of several common laboratory strains of mice which were in no way remarkable as to their body size. From one segregating foundation stock eight successive generations of selections for body size have produced: (1) a race of small body size; and (2) an exceptionally large race, whose individuals average a fourth larger at birth and twice the weight of the small race at 60 days of age.

Size was judged from the 60-day weight, and selections were based on progeny tests, sib likeness and individual phenotype.

The races diverge each generation, but at a lessening rate. Their size distributions show little or no overlap, and the present difference between the races exceeds the mean weight of the small race.

Less grams of body weight were lost by the minus selections than were gained by equal effort at plus selection; and less grams were gained or lost by females than by males.

When measurements are transformed to a percentage or a logarithmic scale the weight gains and losses become approximately equal in both sexes and races.

These data agree with the view that size genes or modifiers multiply each other's effects (that is, act geometrically), and do not simply add to or subtract from the body weight some definite and constant number of grams.

THE DOMAIN OF ETHNOBIOLOGY[1]

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SCATTERED data bearing on the utilization of plant and animal life by primitive peoples in the New World have been accumulating ever since the first voyage of Columbus, but the first attempt to present a systematic statement of the subject appears to be that of Palmer (1870), who published a paper, the content of which was enlarged in a second treatise (Palmer, 1878).

As early as 1875, Powers (1873–74) made an attempt to delimit the field when, in an article entitled "Aboriginal Botany," he employed the term to embrace "all the forms of the vegetable world which the aborigines used for medicine, food, textile fabrics, ornaments, etc." These papers by Palmer and Powers stimulated a considerable amount of interest, as indicated by the appearance of a succession of papers by such men as Powers (1877), Matthews (1882, 1886), Havard (1884, 1895, 1896), Newberry (1887), Coville (1892, 1897), Bourke (1895), Fewkes (1896), Hough (1897, 1898), Barrows (1900), Jenks (1900), Chestnut (1902) and Cushing (1920). Two additional factors contributed materially toward the creation of a deep interest in the aboriginal utilization of plant and animal products. The first was the botanical surveys made in the western United States by representatives of the Federal Government, which brought men into contact with primitive peoples and their methods of exploiting local flora and fauna. The second factor was an exhibit at the World's Fair in 1893 of archeological specimens, such as objects of food, dress, household utensils, etc., from Mancos Canyon, Colorado. At the close of the fair, the University of Pennsylvania secured the loan of this collection.

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[1] The author is greatly indebted to Dr. Leslie Spier for carefully reading and criticizing the manuscript.

The Mancos Canyon collection was studied by Harshberger, of the department of botany at the University of Pennsylvania, who described the objects of vegetable origin; and on the basis of this he delivered a lecture before the University Archaeological Society in 1895, publishing the lecture in the following year (Harshberger, 1896). This apparently represents the earliest application of the term "ethnobotany," which now has come into universal use in America. Schiemann (1932) has summarized some of the related ethnobiological material for the Old World, but neither the term ethnobotany nor any cognate term appears to have been employed in the eastern hemisphere. Although Harshberger indicated several directions in which ethnobotany could be of service, he made no specific attempt to define the term, evidently visualizing it in this and other papers as merely the use of plants by aboriginal peoples. About fifteen years after the publication of Harshberger's first paper, Robbins *et al.* (1916) expanded this concept, pointing out that ethnobotany consisted of far more than collecting, identifying and ascertaining the uses of plants by primitive peoples; that it must strike more deeply into the thought and life of the peoples studied, gaining from them their impressions of total environment involving such matters as primitive concepts of plant life; the effect of a given plant environment on the lives, customs, thoughts and everyday practical affairs of the people studied; and the extent of a people's knowledge of plant parts, functions and activities.

Specific studies on the aboriginal utilization of animal life have been less numerous than those on the plant side, and the data relating to the former have not been so well assembled and organized as have those on plants. Henderson and Harrington (1914) published a paper in which they employed the term ethnozoology as coordinate with the older name ethnobotany. Although this work seems to have stimulated little research into primitive animal utilization as such, a very considerable body of information bearing on the use of animals by primitive peoples is to be found in a variety of publications, which have not been written as special treatises on ethnozoology as, for example, papers by Merriam (1905, 1926), Steensby (1917), Birket-Smith (1929, 1936), Allen (1876) and Hornaday (1889).

For many years, ethnobiological information has been gathered by men with little or no training in the study of the primitive utilization of plant and animal life, and in a manner only incidental to their major fields of investigation with no thought of pursuing such studies for their own sake. The data of ethnobiology, therefore, are scattered in the publications of a wide variety of fields. More recently, a few scholars have adopted ethnobiology as their principal field of interest, and have devoted sustained attention to such studies; as a result we now have in the New World a few professional ethnobiologists, and the field is rapidly taking on the earmarks of an independent line of inquiry, as indicated, among other things, by the recognition which *Biological Abstracts* has given to it within the last few years.

A very large proportion of the ethnobiological investigation in the western hemisphere has been carried on with no reference whatever to a motivating point of view. In the past, and to some extent at present, many data bearing on the utilization of plant and animal life by primitive peoples have been gathered by anthropologists, who obviously have not had the biological background necessary to identify precisely, or even see any necessity for identifying, the organisms in question. This situation often has rendered their data of little value to the biologists. On the other hand, ethnobiological data have just as frequently been gathered by biologists who, completely lacking anthropological training, have, during the course of their investigations, secured no data relative to the importance of these organisms in tribal economy, their manner of utilization, etc. Their publications, constituting little more than a technical list of organisms used by a given people, are dry and barren, and are almost entirely without significance to any one but the botanist.

In view of the above situation, the ethnobiologist is constantly confronted with the problem of delimiting his attitude toward his field of investigation, of defining his point of view or "center of gravity." This, in addition to the rapid progress made in ethnobiology during the last decade, and the recent emergence of the subject as a rather distinct field of inquiry, have motivated several investigators to attempt to circumscribe and define the field of ethnobiology, more particularly ethnobotany.

Vestal and Schultes (1939) have employed the term *economic botany* "to include all plants or plant products of use to man," stating that, in this sense, economic botany is more inclusive than ethnobotany, "a term by which most investigators have designated the plants used by aboriginal peoples." They have adopted what they regard as the broader term, economic botany, "because not all the uses of plants by primitive people are of necessity aboriginal in origin." More recently, Schultes (1941) has reiterated this point of view, stating that the men of science of one or another school are agreeing rather unanimously to regard ethnobotany as "the study of the relations which exist between man and his ambient vegetation." It would seem, however, that Schultes has stated a situation which does not exist in fact, for there is by no means universal agreement with the point of view as set forth by Vestal and Schultes. Economic botany, to be sure, does at times inquire into the relations between primitive man and plants, but rarely does it do so because of any interest in such primitive relationships for their own sake. The major interest of economic botany is in the relationships between plants and modern or contemporary civilizations, and its only interest in primitive relationships consists in the illumination which they may throw upon the modern scene. Ethnobotany, on the other hand, is concerned primarily with the interrelationships between *primitive* man and plants. Moreover, ethnobotany is sharply differeniated from economic botany in that it is vitally concerned with the fundamental *cultural* aspects of plant utilization, while economic botany practically ignores the cultural except in a very general way. One need only to consult any text-book or reference book on economic botany to realize that its major interest consists in treating the importance of plants and the nature of plant products in relation to modern man; in exploring the uses to which plants are put as, for example, foods, oils, waxes, fibers, rubbers, resins, etc., including the study of the morphology of plant parts which produce such structures. Therefore, ethnobiology is to be looked upon as a field of investigation which exists in its own right rather than as a branch of economic botany.

Recently Jones (1941) published an excellent article entitled "The Nature and Status of Ethnobotany" which is noteworthy for two definite contributons; (1) clearly defining and delimiting ethnobotany; (2) indicating how ethnobotany touches related disciplines and discussing the problems which have arisen from such contacts. He defines ethnobotany as "the study of the interrelations of primitive man and plants," and emphasizes that it deals exclusively with the interrelations of *primitive* man and plants and "takes for its sole aim the illumination of this contact." The author fully endorses Jones's definition, which, in addition to circumscribing the field of ethnobotany, inherently demarcates it from economic botany.

Neither Jones's paper nor any other purporting to define ethnobotany has presented a point which seems vital in delimiting the field. This is the question as to what shall be the point of view, the "center of gravity," of ethnobotanists toward the subject-matter of their own field. Ethnobiology[2] has many facets and abuts on a number of disciplines, but for the most part it may best be regarded as marginal to, or as straddling, both biological science and anthropology. It utilizes the data and the methods of both fields. The question therefore naturally arises as to whether this "center of gravity" shall be biological or cultural or a combination of the two. The author does not look upon ethnobiology as a distinct science and discipline, but rather as a sphere of investigation in which scholars, trained in both biology and anthropology, can render a service to the two fields which neither biologist nor anthropologist as such would be competent to contribute.

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[2] From this point on the discussion will bear on ethnobiology rather than on ethnobotany, for the comments apply equally well to both plant and animal life.

There exist certain purely biological aspects to ethnobiology, such as the identification of organisms and their parts as employed by primitive peoples. Often, as in the identification of plant and animal archeological specimens, the situation calls for special and ingenious techniques, sometimes highly refined. Despite the biological aspects of this problem, which involves a knowledge of such things as plant and animal anatomy and geographical distribution of organisms, an anthropological background also is very useful in making such specific determinations of ethnographic or archeologic specimens. Thus, knowledge of the people among whom a particular specimen was collected, the physiography of their range, their food habits, relations with other peoples, etc., are of considerable aid in identification, even if they consist only in eliminating certain organisms from consideration.

When the average person knows that a specific plant or animal was used by a given primitive people, he is by no means content to stop there. It is a thoroughly human quality to inquire what the organism was used for, precisely how it was utilized, the antiquity of its utilization and what the people who employed it were like. When a plant is seen growing in nature, knowing its name may go a long way, if not the entire way, toward satisfying the average person's interest in it. But when it is found in association with coal, a peat bog, an archeological ruin, a Papago storehouse or poisoning fish, it assumes an entirely new significance. What the botanist has to say about a plant no more exhausts what there is to be said about it than his description of a flower represents all there is to be said about that very interesting plant structure. But just as soon as one begins to answer the questions posed above, he is getting over into the anthropological, the cultural. The availability of a specific food may even determine modes of Indian settlement. Thus Papago families moved annually to the nearest available giant cactus forest to live on saguaro fruit for a period of several weeks when this fruit was ripening. Similarly, Lowie (1940) has pointed out that mode of settlement in the Great Basin area hinged on the supply of piñon nuts. Since a good crop was too large for transportation winters had to be spent near the storage places. In the same manner, Spier (1930) has pointed out that the Klamath Indians in Oregon customarily left their winter villages in April or May to catch fish, gather camas root, etc., and did not return until the snow fell.

Despite the many biological aspects of agriculture, a study of the *origin* of agriculture is much more of a cultural than a biological problem. The biologist's contribution regarding knowledge of the plants used in ancient agriculture leaves a great deal unsaid about primitive cultivation. A study of early Pueblo agriculture, for example, reveals that its crops and techniques simply can not be investigated apart from their ceremonial aspects. The two are wholly inseparable. The real history of agriculture must be economic and social and must have much to say about the "human soil," the social and economic conditions out of which agriculture grew. The first steps in the initial developement of agriculture must have been economic and social, rather than botanical. As regards the cultivation of maize in the American Southwest, in ancient times both flour and flint varieties were grown. To the average observer, it would make little if any difference as to which type a certain people grew. The genetical and botanical differences between flour and flint maize are quite small, for the change from flint to flour corn is controlled by a single gene difference, but the cultural differences associated with the two are great. Primitive Indian groups in the Southwest ground their corn to meal with metate and mano. Even the grinding of flour corn was a slow, laborious process, but the labor involved in grinding flint corn would have been increased many fold. Hence a people limited to the growing of flint corn, for whatever reason, might utilize the crop in ways other than first grinding it to make flour. The type of practice necessarily influenced not only economic but social life, for if a woman had to spend four hours a day grinding flint corn while she could secure the same amount of meal by grinding flour corn only two hours a day, this necessitated a redistribution of her time and thereby had an effect upon the life of the whole family.

In connection with this cultural point of view, it is worthwhile to point out that this subject is also of considerable interest to the geographer. There exists in some quarters a common opinion that, if one knows the geography of a people's habitat, he can state just what wild plants and animals this people used for food, etc. While it is true, in a broad sense, that the material controls of activities based upon the vegetable and animal worlds lead to broad distinctions in the economies of primitive peoples, amounting to geographic determinism in a degree, culture involves much more than geography. Geography limits culture, but by no means is it its sole determinant. While it is valid that, in general, the utilization of food sources is a rational process, varying with their abundance and availability, there are many exceptions. The satisfaction of subsistence needs by a given people is often very irrational, and arbitrary food habits and preferences, dictated by taste and tradition, do exist. Thus such utilization is frequently determined culturally rather than ecologically. Knowing what available and suitable floral and faunal elements a people do not utilize from their natural environment often is just as significant as knowing which ones they do employ. For example: There is no logical reason why any available food should have been completely excluded from a people's diet. Yet, some of the Northwest Coast tribes, such as the Kwakiutl on Vancouver Island, would not touch venison, even though deer were abundant in their territory. Spier (1930) has pointed out that the Klamath Indians' leaning toward fish as their staple and their relatively small use of deer, elk, antelope and waterfowl, all of which abound in this territory, are arbitrary and not dictated by geographic conditions; and that their food habits are such primarily because they share the habits of the Columbia-Snake river tribes as a whole. That abundance in itself does not guarantee utilization, or at least extensive utilization, is seen again among the Klamath. In addition to the bountiful supply of game in their territory, these Indians had available in Klamath Marsh, according to Coville (1904), the seeds of about ten thousand acres of wokas or the great yellow water lily (*Nymphaea polysepala*), only a small fraction of which was utilized. Despite this plenitude of food, travelers among the Klamath in the early nineteenth century frequently referred to the fact that in winter these Indians were often on the verge of starvation. This was not due to improvidence. For example, the period during which wokas seed could be harvested lasted only a very few weeks, and the process of seed preparation was slow and tedious. This, coupled with the difficulty of transporting the seeds, rendered it impossible to gather, prepare and store large quantities of wokas. Moreover, it is no easier to undertsand why a particular food should be exploited to the wide exclusion of all others, even though abundant, as was the acorn in much of California.

A study of the utilization of specific plants or animals by certain primitive peoples not only shows correlations between culture and terrain, but sometimes furnishes valuable clues to historical circumstances. It may not only throw light on the diffusion of certain plants but on the histroical diffusion of culture in general. This is nicely illustrated among the Crow Indians of southeastern Montana.

The Blackfoot and the Sarci of the northwestern Plains are the only tribes which share with the Crow the ceremonial planting of tobacco, and this represents the only agricultural effort of these typical bison hunters. Lowie (1920), in discussing the Tobacco Society of the Crow, points out that, as an *organization*, this society is an independent structure, presumably of indigenous growth among the Crow, even though some of its elements have their origin among other tribes. Despite the fact that the elaborate organization of the Crow Tobacco Society is without parallel among the Blackfoot and Sarci, the resemblances between the planting performances of the three tribes suffice to establish ultimate community of origin for the practise. The question naturally arises as to whether the Crow borrowed from the Blackfoot (and the marginal Sarci) or *vice versa*. For the reasons which follow, Lowie concludes that the Crow derived their tobacco agricultural technique from the Hidatsa (living on the upper Missouri), elaborated it ceremonially, and subsequently transmitted it to the Blackfoot, who in turn passed it on to the Sarci together with some of the ceremonial patterns which the Blackfoot themselves evolved: (1) the much more important place which tobacco planting holds among the Crow than among the Blackfoot; (2) the Crow were intimately related to the Hidatsa, who planted tobacco, as well as corn, beans, pumpkins and sunflowers, while the Blackfoot were not in contact with any group from whom they could be expected to have derived the technique; (3) the only Siouan language in which the Crow stem for "tobacco" appears is Hidatsa (*ōpe*). Anthropologists believe there is considerable evidence that the Crow and the Hidatsa were one people not so very long ago, one important consideration being the close similarity of language. Reasons nos. 2 and 3, as presented, shed some light on the historical diffusion of a cultivated plant, of a culture trait and even of the movement of a people itself; that the Hidatsa share with the Crow a common term for tobacco, as well as an agricultural technique, provides bits of evidence in support of the thesis that these two peoples formerly were one. The fact that the Hidatsa cultivated *Nicotiana quadrivalvis,* in non-ritualistic fashion, while the Crow grew *N. multivalvis,* and only ceremonially, does not vitiate the conclusion that the Crow borrowed their tobacco-growing technique from the Hidatsa and elaborated it ceremonially.

Out of the author's experience in ethnobiology have come certain definite conclusions regarding factors to be kept in mind in carrying on research in this field. These apply particularly to the study of wild plants and animals, although some of them are equally applicable to the investigation of domesticated forms. The student of cultivated plants and animals and of primitive agriculture is advised to consult several of the better treatises on these subjects before undertaking field studies relating to them.

(1) Identification, in exact taxonomic terms, of the plant or animal used. This is less easy with animals than with plants because of the difficulty of obtaining and preserving specimens. In any case, if the investigator is himself not competent to make the exact identifications, he should seek the assistance of specialists.

(2) Relative abundance and availability of the organism.

(3) Indian name for the plant or animal. This often gives an insight into the tribe's conception and knowledge of the structure, function and method of classification of organisms, as well as into related aspects of the people's ceremonial life. Moreover, this name is often of much practical aid in identification when only fragments of the plant or animal are available for study.

(4) The part of the organism utilized by the natives, *i.e.,* root, stem, leaf, flower, seed, etc.

(5) The purpose for which the plant or animal or part thereof is utilized.

(6) The exact manner in which the organism or the part used is prepared.

(7) The season in which the plant or animal is collected by the natives. This contributes toward working out the calendric sequence or annual cycle with respect to economic life.

(8) Whether or not the organism is native to the area inhabited by the people under consideration.

(9) The antiquity of utilization. It is of the utmost importance to ascertain whether or not such employment of a specific organism is aboriginal.

(10) The actual value by modern standards of the plant or animal employed. This applies particularly to the study of plants used medicinally and involves an inquiry into the actual therapeutic value of the plant. Frequently such information is not available in our own materia medica and would call for pharmaceutical research, which of course lies outside the purview of the ethnobiologist.

(11) What species of plants and animals in the tribe's environment are not utilized. For example, as indicated above, some tribes ignore major, readily available food sources. Such facts are significant, call for explanation and may illuminate certain cultural relations.

(12) Importance of a specific plant or animal in the tribe's economy. Frequently, published papers merely state that a people utilized a certain organism, and such information is practically worthless. It is of the utmost importance to weigh the value of specific plants and animals in exact terms, if possible, otherwise relatively. The ideal would be to ascertain, for example, whether a given wild or cultivated plant constitutes 5, 30 or 70 per cent. of a tribe's total food supply.

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REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

In this section reviews and notices are given of current publications on general biology and of specialized works which have an important bearing in this general field. Emphasis is given to books and major articles which fall within the special scope of The American Naturalist, in that they deal with the factors of organic evolution.

Reviews and Comments are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

Finger Prints, Palms and Soles. By HAROLD CUMMINS AND CHARLES MIDLO. Philadelphia: The Blakiston Co., **1943**: i–xi, 1–309, frontisp., figs. 1–149. $4.00.

THE value of finger prints in individual identification is widely recognized. Their biological significance, as well as that of palms and soles, has been just as widely neglected, even by the majority of biologists. Nevertheless, in studying these characters, some few scientists, since the time of Francis Galton, have uncovered fascinating and surprisingly large amounts of information bearing on problems of embryology, physical anthropology, genetics and evolution. The general lack of interest in and knowledge of dermatoglyphics has likely, in no small measure, been due to the lack of any book or journal comprehensively dealing with the various aspects of the subject. This lack has recently been eliminated in an admirable manner by the publication of Cummins and Mildo's new book, "Finger Prints, Palms and Soles."

The book consists of three parts: I, Orientation; II, Methodology and Description; and III, Biology. Parts I and II acquaint one with the history and techniques of dermatoglyphics. Part III gives a very complete and comprehensive discussion of the various aspects of dermatoglyphics, of interest to biologists. Practical applications, as in twin diagnosis and questioned paternity, are carefully considered. The chapters on comparative dermatoglyphics, embryology, symmetry, inheritance, racial variation and constitution furnish an abundance of material which should be of interest to the student of evolution. The following paragraphs give a brief résumé of some of the authors' conclusions:

The pattern areas are elevated regions on finger-tips, palms and soles. These are homologues of the primitive volar or walking pads of other mammals. The epidermal ridges are derived from scales, each of which was associated with a sweat gland and a hair. During the evolution of the epidermal ridges the hairs disappeared, and the scales aggregated into ridges. Some degree of ridge formation is manifest on the volar pads of all primates. The degree of pattern development is positively correlated with the degree of volar pad elevation. In both palms and finger-tips the evolutionary trend has been from high pattern intensities to patternless configurations. Of pattern types, elliptical whorls are the most primitive, followed by circular whorls. Arches are the most specialized. At the close of the second month of embryological development the volar pads of the palm and fingers appear as localized bulges, and during the ensuing four weeks become more rounded and individualized. At about the thirteenth week these pads begin to recede and become more indefinite. Pads of the sole develop and recede about two weeks later than those of the hand. Epidermal ridges of the fingers are differentiated during the third and fourth fetal months, and elevated on the skin surface at about eighteen weeks. Finger ridges appear first and sole ridges last. If a pad does not completely recede before ridge information, a pattern will be formed in the area. If it does recede before ridge formation, the area will likely be patternless. The three great apes and man present specializations which follow different directions. The evidence indicates that man stemmed from an ancestral stock more primitive than any recent ape, having dermatoglyphic traits more closely allied to those of monkeys.

Genetic factors are responsible for much of the variation in dermatoglyphics, as evidenced by the great intrapair similarities of identical twins, and lesser similarities between less closely related individuals. The genetics of the pattern intensity variations in finger-tips is the most thoroughly understood, although the inheritance of certain variations in finger pattern shape and the occurrence of thenar-first interdigital patterns appear to be fairly simple. Interracial comparisons manifest marked differences in gene frequencies. Accepting whorl-loop-arch as representing successive departures from the primitive, finger prints of the yellow-brown human races are the most primitive. The most specialized are certain components of the black, and among whites, the Nordics. Geographically in Africa, Asia and America there is a tendency towards reduction of pattern intensity from north to south, whereas in Europe the line of pattern reduction is from south to north.

Dermatoglyphics are differentiated by the end of four months of fetal development and undergo no further changes, except in total size, during the life of the individual. Consequently, any associations between dermatoglyphics and constitutional types are indicative of differences existing during early fetal development. Several such associations are known. Patterns show consistent differences in their occurrence on right and on left hands. Populations of left-handers show a reduction of bimanual asymmetry, as contrasted with populations of right-handers. Males show greater variability than do females. The dermatoglyphics of Mongolian idiots deviate markedly from those of normal individuals. Finger-print trends also appear to be aberrant among victims of neurofibramatosis, schizophrenia and epilepsy.

The book is amply illustrated. A bibliography at the end includes 361 references. The appearance of "Finger Prints, Palms and Soles" should do much to stimulate interest in this field, so rich in biological significance, which in the past has often been overlooked or neglected.

D. C. Rife

Taxonomy and Phylogeny. By W. B. TURRILL. Bot. Rev., 8, 1942: 247–270; 473–532; 655–707.[1]

WHEN a long-felt need has been successfully met the achievement certainly deserves recognition. In the opinion of the present writer, this review of Turrill's does meet a real need on the part of younger students who desire orientation in the maze of plant classification as well as older ones, most of whom have concentrated more or less narrowly on the systematics of certain groups of organisms. Although the title is general, the author is a botanist and "conclusions or opinions of zoologists are quoted only when they supplement or contrast with those of botanists." The review consists of three parts.

Part I, after an illuminating discussion of the derivation and meaning of terms, especially taxonomy and phylogeny, briefly reviews the historical development of plant classification, from pre-Linnaean to post-Darwinian systems. Part II reviews (1) taxonomic and phylogenetic concepts and criteria; (2) data used in classification and phylogenetic studies. Part III presents (1) a brief discussion of each of the major groups of both cryptogams and phanerogams; (2) general considerations and conclusion.

It is impossible in a brief note to give an adequate notion of the content of this paper. No serious student of systematics can afford to ignore it and, for all younger students in this field, it may well serve as an introductory text. The amount of literature covered is extensive and truly representative in each of the several fields. The organization is logical, the style is clear and readable, and the author's interpolations of his own ideas and opinions are critical and constrained. There is much of interest to any biologist who is at all concerned with evolution.

Certain parts that particularly interested the present writer are: Darwin in the history of plant classification, pp. 264–266; the species concept, pp. 479–482; princip of phylogeny, pp. 488–495; data used in classification and phylogeny, pp. 496–532; and discussion of "logical as opposed to phylogenetic classification," pp. 676–684.

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[1] This contribution inadvertently failed to receive current review in our columns, but is judged to be of such great significance as to warrant this belated notice.—C. L. H.

The last-mentioned topic is in itself somewhat unfortunate since it implies that no phylogenetic classification can be logical, which is not necessarily true. But the discussion which follows is a sane, well-balanced evaluation of the general problem of maintaining a *practial* system of nomenclature for organisms and at the same time giving due regard to the generally accepted principle that these organisms have evolved and are now evolving. Quoting Turrill's concluding paragraph:

> The task of the systematist is twofold: to prepare as many special classifications as are needed for special biological investigations, or to make available materials for others to construct such special classifications, and to make a general classification which shall express as far as possible in rational order all that is known concerning plants and animals. This last is an ideal which, even if never attained, is one which may well make the systematist proud in the magnitude of his task. It is an ideal greater than the phylogenetic ideal which is included in it and one which in the process of attempted attainment must make taxonomy what it should be, the focal point of biology.

E. B. BABCOCK

NOTICES OF NEW BOOKS

A Cytological Study of *Crepis fuliginosa, C. neglecta,* and Their F_1 Hybrid, and Its Bearing on the Mechanism of Phylogenetic Reduction in Chromosome Number. By H. A. TOBGY. Jour. Genetics, 45, 1943: 67–111, pls. 1–3, figs. 1–74.—Dysploid series of chromosome numbers, such as 6, 5, 4, 3, among closely related species have been assumed to arise through translocations between non-homologous chromosomes followed by the loss (or addition) of a chromosome pair (Navashin's "dislocation hypothesis"). Until now the only evidence in support of this hypothesis is Dubinin's experimental production of a 3-paired form of *Drosophila melanogaster* (cf. Biol. Zhur., 3, 1934: 719–736). The first supporting evidence from plants was found by Dr. Hassan A. Tobgy of the Egyptian University, Cairo. From a careful analysis of meiotic phenomena in F_1 hybrids between two wild species, *C. fuliginosa* ($n=3$) and *C. neglecta* ($n=4$), Tobgy has been able to show that two chromosomes, designated B and C, in the 4-paired species are represented by just one chromosome (B) in the 3-paired species. The reduction in number is assumed to have come about through unequal reciprocal translocation between the B and C chromosomes of *C. neglecta,* in such a way that the C centromere was left with only genetically inactive chromatin attached to it, and through the eventual loss of this C centromere. Additional evidence supporting this assumption is presented. Coming from natural species in a genus where progressive reduction in chromosome number is the general rule, this achievement reveals the most probable cause of dysploid series in general. The Division of Genetics of the University of California, where the research was done, will be in position to supply reprints to those who care to apply for them.—E. B. BABCOCK.

An Analysis of Mink Predation upon Muskrats in North-Central United States. By PAUL L. ERRINGTON. Res. Bull. Agri. Exp. Sta. Iowa State Coll., 320, 1943: 797–924, figs. 1–16.—Although undertaken primarily as an investigation in the field of wildlife management, this research like others by the same author penetrates deeply into the philosophy of predation and bears directly on problems of population analysis and indirectly on problems of speciation. "It was found that strangeness of environment, intraspecific intolerance, and drought were especially important in predisposing muskrats . . . to predation . . . ; and that kinds and numbers of wild predators doing the preying, with a few apparent exceptions, had little bearing upon the net mortality. . . . For reasons of intercompensatory (automatically adjusting) trends existing in reproductive as well as loss rates of the muskrats, severity of predation . . . may leave highly misleading impressions as to population effect. Even when locally nearly annihilative, predation rarely showed evidence of functioning as a true population depressant, insofar as it usually only took the place of some other mortality factor." Opponents of the theory of natural selection, like McAtee, may find in such studies support for their position. If loss to a predator merely releases the need for intraspecific population control, if the prey becomes invulnerable to predation but continues to exist under severe predation loss, if it is inconsequential which species of predator is doing the preying, and if removal of predators will have little effect on the populations of the prey, then what significance can be attached to any protective device, such as concealing coloration or special habits, which seems to have been evolved to prevent the destruction of the species by any one predator, or by predators in general? Here's something to think about. Obviously the life or death of a species depends on a highly complex adjustment to a multitude of potentially destructive factors. Perhaps one of the leading adaptations has been the perfection of the "intercompensatory trends."

Northern Fishes With Special Reference to the Upper Mississippi Valley. By Samuel Eddy and Thaddeus Surber. Minneapolis: University of Minnesota Press, 1943: i–xi, 1–252, frontisp., figs. 1–57 (4 col.), diags. 1–3. $4.00.—"Northern Fishes" will help ichthyology to catch up with other phases of American vertebrate zoology. Though it was written as a Fishes of Minnesota, it will be needed by every student of the fishes of any part of eastern North America, and warrants a good sale among general naturalists and among sportsmen. The introductory chapters are well written. The nomenclature is up-to-date and the general statements on characters, habits and on distribution are valuable and interesting. The authors hit a good batting average of accuracy, though minor misstatements and omissions will be occasionally apparent to the specialist. The greatest scientific contributions perhaps lie in the analyses of the distribution of the various species in Minnesota. Of most general biological interest is the account of the silver pike, a true-breeding mutant of the northern pike which has appeared in recent years in a number of Minnesota lakes. This peculiar fish is beautifully illustrated in color, along with a muskallunge. The three other colored plates are hardly up to modern standards. The numerous photographs, however, are singularly successful in portraying specific characters.

The Green Earth An Invitation to Botany. By Harold William Rickett. Lancaster, Pa.: Jaques Cattell Press, 1943: 1–350, many figs. $3.50.—One of the Humanizing Science Books of The Jaques Cattell Press, "The Green Earth" is offered as "a layman's guide to botany." For this purpose it is beautifully written, with skillful choice of plain words, with lucid descriptions and with impressive figures of speech. It would, for example, be difficult to find a better-worded statement on the search for the basic principle of life than this: "Biologists and philosophers, each in turn misleading the other, have trampled the ground into a morass upon which it profits not to venture." The author's competence as an artist does not end with his word pictures, for he has very attractively illustrated his book with pen and pencil sketches of plants and their parts.

When early in the reading I encountered the false statement that the smallest fish live on the plants, I began to look for further errors, but soon ended the search with the conviction that the text is marked by accuracy as well as beauty. Nontechnically but reliably the competent author writes of photosynthesis, of leaf anatomy, of the architecture of plants, and of their growth; inserts the philosophical chapter, "Of the Purposes of Plants," from which the quotation is taken; then describes flowers and fruits, plant genetics, and plant nomenclature; finally races through a discussion "Of Fern and Moss" and of seed plants, to finish with "The End of Things" and a thoughtful Epilogue.

Manual of Comparative Anatomy. By OSMOND P. BRELAND. New York and London: McGraw-Hill Book Co., 1943: i–ix, 1–250. $2.00.—Text books and laboratory manuals in comparative anatomy keep coming from the press in a seemingly endless flow. This is a good manual—like many of the others. The very explicit instructions, especially for the drawings, will save the student from any need for mental effort or originality in planning his work, and will lighten the instructor's load. The treatment is purposefully conventional in vertebrate classification and is similarly conservative in anatomical and systematic nomenclature. The dogfish is stressed, as a simple example of fundamental vertebrate organization; amphioxus, lamprey, perch, *Necturus* and turtle are treated in less detail. Lastly the cat is accorded more attention, as an example of mammalian anatomy. Occasional paragraphs help justify calling this a manual of *comparative* anatomy. There are no illustrations. The typography is beautifully clear and the reduced over-all size of the page, though pardoned as a required war economy, strikes me as an advantage.

Vertebrate Photoreceptors. By SAMUEL R. DETWILER. New York: Macmillan Co., 1943: i–x, 1–184, figs. 1–110. $4.00.—"The eyes have it." Excellent general treatises on the vertebrate eye and on vision continue to appear. Among the more recent (1941–1943) items, four may be singled out for mention. The 1941 contribution, "Vision A Study of Its Basis," by S. HOWARD BARTLEY (New York: D. Van Nostrand Co., 1941: i–xv, 1–350, figs. 1–77. $3.50), is a well-documented handbook emphasizing the marked advances of the past decade in the physiology of vision. In 1942 two outstanding volumes appeared: "Visual Mechanisms (Biological Symposia, Vol. VII, noticed in the September-October, 1942, number of THE AMERICAN NATURALIST) and "The Vertebrate Eye and Its Adaptive Radiation," by Gordon L. Walls (reviewed in our columns for January–February, 1943).

The most recent of these books is Detwiler's Vertebrate Photoreceptors. It is issued in the Macmillan series of Experimental Biology Monographs, but gives at least as much attention to comparative anatomy and histology of the eye as to physiological experiments. Bartley's book on Vision is not referred to, and Wall's compendium is barely mentioned. Technical contributions, however, are extensively cited. Detwiler's expressed aim has been "to present a general account of the visual cells of vertebrates, with particular emphasis upon their development, structure, distribution, and certain aspects of their physiology." He pays particular attention to the duplicity theory, which has been sustained, he thinks, by quantitative researches on the major functions of vision: dark adaptation, intensity discrimination, visual acuity and flicker responses. He summarizes researches on these functions, stressing in particular Crozier's recent work on flicker responses. He also emphasizes the researches by Wald on the visual pigments and their relation to the A vitamins.

Microscopic Technique in Biology and Medicine. By E. V. COWDRY. Baltimore: Williams and Wilkins Co., 1943: i–iv, 1–206. $4.00.—Concentration and organization are key features of this handbook. Beyond the brief introduction, dealing with choice of methods, organization of laboratory and standardization of stains, the subject matter is arranged alphabetically. Here one will find under the names of stains, fixing agents and other chemicals, brief statements as to their use; under anatomical and cytological terms, suggestions for effective treatment; under animal names, techniques particularly suited to the given group; under authors' names, special methods proposed by these technicians. Throughout, the statements are marked by clarity and brevity, and are abundantly documented by references to the source literature. Cross references are frequent. Only a great, productive investigator would have conceived such an arrangement, or would have done the job so well. Outstanding is the stress on new methods, which are based on recent advances in physics and chemistry and which are opening new avenues of research and interpretation.

Frontiers in Cytochemistry The Physical and Chemical Organization of the Cytoplasm. Edited by NORMAND L. HOERR. Biological Symposia, Vol. X. Lancaster, Pa.: Jaques Cattell Press, 1943: i–vii, 1–334, frontisp., pl. 1, 98 figs. $3.50.—What finer monument could a scientist want, than a printed symposium like this one, dedicated to him out of deep respect for his pioneering and his leadership in a fundamental field of research? Particularly fine is the indication that the recipient of this honor, Dr. R. R. Bensley, has made some of his most notable contributions during the decade following his retirement to an emeritus professorship. May his example be emulated!

This symposium presents the results of the epochal advances made during the past few years in the knowledge of the physics and chemistry of cytoplasm—advances due largely to Bensley's active participation and intellectual leadership in the research, to his constant search for new analytical methods and to his insistence on maintaining the cellular elements in as little modified and as little disorganized a condition as is consistent with their separation and analysis. Outstanding elements in this advance include the mass separation of mitochondria, the recognition of such bodies as the submicroscopic lipoprotein complex and particulate glycogen, and the actual discovery of the theoretically assumed micellar components.

An Introduction to Biophysics. By OTTO STUHLMAN, JR. New York: John Wiley & Sons, 1943: i–vii, 1–375, 154 figs. $4.00.—In these days of integration of sciences, special education in the boundary fields becomes increasingly important. This text provides for training in biophysics. It is written by a physicist, but the text as well as the bibliographies which accompany each chapter are rich in references to biological work. The 8 chapters deal with biophysically active x-rays, applied radioactivity, biophysical characteristics of the eye, emission and absorption of biophysically active light, the structure and properties of surfaces and membranes, the biophysical problem of nerve conduction, auditory biophysics, and lastly, with the compound and electron microscopes.

Why the Universe? Or, Cosmopoietic Space. By PERCY A. CAMPBELL. San Francisco: George Fields, 1943: 1–189. $2.50.—Often when tempted to write disparagingly of a man's printed work I find myself restrained by the attitude of an older investigator when commenting on an author whose treatise might well have been ridiculed. "At least," he said, "his mind has not been stagnating." Certainly no one could accuse the author of "Why the Universe?" of mental stagnation. He starts with the assumption that space itself is the unitary principle of the universe, and believes that space can and must "be given also the all inclusive cosmopoietic role, the role of cosmos maker." Physics and biology, evolution and anthropology, conservation and religion: he discusses them all. And he pictures life as "self-aggrandizing bioprecipitation."

Handbook of Salamanders. By SHERMAN C. BISHOP. Ithaca, N. Y.: Comstock Publishing Co., 1943: i–xiv, 1–555, colored frontispiece, figs. 1–144, maps 1–56. $5.00.—This volume, the best of the "Handbooks of American Natural History," is as momentous to herpetology as was Cope's "Batrachia" (1882) and Blanchard's "Key to the Snakes" (1924). An admirable introduction of some twenty pages, followed by an account of the species and subspecies, is buttressed by the index and an excellent 67-page bibliography. One hundred twenty-six species and subspecies are recognized, including 100 of the 102 recognized in the Stejneger and Barbour "Checklist" of 1939.

That the author knows and is in sympathy with his subject and that he has not been commissioned to present it is refreshingly apparent throughout. Although the manuscript was in preparation for many years there is nothing labored about the finished product.

For the systematic accounts, the life-histories, the keys, the many and excellent illustrations the reviewer has only the highest praise. The outstanding faults of the fine handbook all concern the distribution maps, which are ill-chosen in regard to size, composition and symbols. Maps showing actual locality records would have been much more serviceable and thought-provoking than the general distribution maps, often misleading, employed in this volume. Whether a map portrays a restricted distribution of a single form or the widespread distribution of several forms the type and size of the maps are the same. Indications of latitude and longitude are omitted. The choice of maps was apparently haphazard, for of the 56 maps, 35 show the major rivers of the areas portrayed while these features for no apparent reason are omitted on 21.

These minor faults detract but little from the immense value of the book. Certainly every herpetologist must have a copy and every naturalist should.—NORMAN HARTWEG.

GENETICS SOCIETY OF AMERICA

THE Genetics Society of America announces that the following officers have been elected for 1944: President, Professor A. H. STURTEVANT, California Institute of Technology, Pasadena; Vice-President, Dr. B. P. KAUFMANN, Carnegie Institution, Cold Spring Harbor, New York; Secretary-Treasurer (for a term of three years), Professor LAURENCE H. SNYDER, Ohio State University, Columbus. These three officers, together with the two most recent past presidents of the society, Professor M. M. Rhoades, Columbia University, and Professor E. W. LINDSTROM, Iowa State College, constitute the Executive Committee for 1944.

A recent survey conducted with a view to revising the directory of the society shows that about ten per cent. of the members are now serving in the armed forces, and that a considerably larger number are engaged in scientific work directly related to the war effort. No formal meetings of the society have been held during the past two years, although other activities, including publication of the "Records," continue. The current issue (No. 12) of the "Records" contains, in addition to the directory of members and reports on the activities of the society during 1943, a series of short papers dealing with recent genetic studies.

B. P. KAUFMANN

SHORTER ARTICLES AND DISCUSSION

THE GENETIC BASIS OF DIFFERENCES BETWEEN TWO SPECIES OF DROSOPHILA

THE problem, whether hereditary differences between different, related species are due exclusively to differences in their chromosomes or whether non-chromosomal, cytoplasmatic elements are involved also, has found various answers. Among plants, convincing evidence has been presented for some cases in support of the view that only Mendelian inheritance by genes is responsible for species differences, while in others extra-chromosomal elements clearly have a share in this determination. In animals few cases have been amenable to treatment, this being largely due to the interference of hybrid sterility, which places a bar before a genetic analysis.

The two closely related species *Drosophila virilis* Sturtevant and *D. americana* Spencer offer suitable material for a test of this nature. These members of the "species complex *Drosophila virilis*" were originally considered subspecies and are so listed by Sturtevant (1942) while Patterson (1943) regards them as distinct species. We shall follow the latter author's designation. While very similar to each other the two forms are morphologically distinct and reproductively strongly isolated (Spencer, 1940, Patterson, Stone and Griffin, 1940, 1942, Stalker, 1942a). Hybrids, however, can be obtained and are partially fertile. This makes it possible, by repeated backcrosses of the hybrids to one of the original species, to obtain individuals in which all chromosomes are derived from this latter species. If the cross is so arranged as to have the cytoplasm of these individuals descended from the other species of the original cross the following alternatives can be decided upon:

(a) The specific differences between *virilis* and *americana* are carried exclusively by the chromosomes. In this case the backcross individuals should completely resemble that species whose chromosomes they contain.

(b) The specific differences are wholly, or partly, due to self-reproducing cytoplasmatic elements. In this case the backcross individuals should retain characteristics of that species, none of whose chromosomes, but whose cytoplasm they contain.

Obviously, the experiment can be arranged in two ways, namely to make either *americana* the cytoplasmatic and *virilis* the chromosomal donor or reciprocally. Only the first type of experiment was carried out, in three parallel sets. In two of them *americana* females in mass cultures, were mated to *virilis* males (of the sepia yellow scute stock), the F_1 females, again in mass matings, crossed back to *virilis* males, and single females of the next generation mated again to single *virilis* males. In the third line single pair matings were used from the very beginning. In all three lines further backcrosses of the type described, in pair matings, were repeated over a period of about two years. At the end of this time three separate lines of “virilized” flies, derived from three original *americana* females, were available. These females came from stocks descended (1) from a single fertilized female collected by H. D. Stalker at Defiance, Ohio, and (2) from another such female collected at Overton, Ohio. The three strains of backcrossed hybrids will be referred to as Ad (from Defiance), Aoa and Aob (each from a separate female of the Overton stock). In order to compare the chromosomally *virilis*-type hybrids with pure *virilis* the experiment was conducted so as to have available a *virilis* stock chromosomally highly isogenic with the hybrids. It was intended at first to establish three separate *virilis* strains each isogenic with a different one of the hybrid strains. Accordingly, the single *virilis* male used in each backcross was also used in a separate culture bottle, in a mating to a single pure virgin *virilis* sister, and the parents of the next generation were taken from among the offspring of the *virilis* male with (1) its hybrid and (2) its *virilis* mate.[1] After from three to seven such separate hybrid female × *virilis* male × *virilis* sister crosses it was decided to make all three hybrid strains isogenic among themselves and with a single *virilis* strain. This goal was approached by the following sequence of single pair matings:

generation “n”	hybrid Ad ♀ × vir ♂ × vir sister
	hybrids Aoa ♀ and Aob ♀ × brothers of above vir ♂
generation “n + 1”	hybrid Aoa ♀ × vir ♂ (F_1 of generation n) × vir sister
	hybrids Aob ♀ and Ad ♀ × brothers of preceding vir ♂
generation “n + 2”	hybrid Aob ♀ × vir ♂ (F_1 of generation n + 1) × vir sister
	hybrids Ad ♀ and Aoa ♀ × brothers of preceding vir ♂

with generation “n + 3” repeating the type of cross of generation “n,” “n + 4” repeating “n + 1” etc. Since this scheme was

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[1] We are indebted to Mr. Lloyd Birmingham, who carried out the initial crosses.

practised for at least 23 generations a high degree of similarity in the chromosomally determined genetic makeup of the three hybrid lines and the *virilis* line must have been obtained. A cytological investigation of the salivary glands in the hybrid lines, while obviously unable to verify isogeneity in its strictest sense, nevertheless confirmed the expectation of at least no appreciable segment of any *americana* chromosome being present. Segmental heterogeneity would have been obvious from the appearance of incomplete pairing of sections of the chromosomes or of inversion loops; however, pairing was normal in the few cases of each line studied.

Comparisons between the three hybrid and the *virilis* lines involved both morphological and physiological characters used in the specific diagnosis of the two species. With the exception of two of these characters, cross-fertility and position of flies, these comparisons were carried out by the one of us (W. P. S.) who first described *americana* and pointed out its relation to *virilis* (Spencer 1938, 1940; see also Stalker, 1942a). A morphological comparison relating to (1) width of cheek, (2) eye pile, (3) eye size and (4) shape of spermathecae yielded no recognizable differences between any of the three hybrid lines and *virilis*. Another character, (5), width of carina, which, due to overlap in the two species, is a less reliable differentiator, also appeared alike in all four stocks. These comparisons were made after 33 generations of single pair backcrosses in the lines Ad and Aoa, and after 29 such generations in Aob (plus the initial two generations of mass matings in Ad and Aob). Since three additional morphological characters, namely (6) body color, (7) eye color and (8) cloudiness along veins of wing, could not be studied in the isogenic lines, owing to the presence of the mutants sepia and yellow, individuals from all four lines were mated to wild type *virilis* from a stock culture and the F_1 flies compared among each other (this outcross was undertaken one backcross generation later than the time of the first comparisons). Again there was every indication that the three hybrid lines were identical to *virilis* and different from *americana*. A striking physiological differentiation between the two species, (9) speed of etherization and recovery from ether, also appeared alike in the hybrids and in *virilis*. The same was true for (10), position of undisturbed adults in culture bottles: Unlike *americana*, which form closely grouped aggregates, the hybrid strains showed the adults in the isolated positions characteristic for *virilis*. All ten specific character differences mentioned can thus be said to be due to chromosomal differences between the two species only. The detailed basis of these differences is unknown, but an eleventh character, coloration of pupae, has been shown by Stalker (1942b), to depend on differentiating genes located in chromosomes (2 . . . 3) and 5 of *americana*.

Since the low fertility of the cross between *americana* and *virilis* furnishes an important argument in the assignment of specific rank to the two forms, a quantitative study was made of the ability to produce offspring in crosses between the hybrid lines and the *virilis* line. Pair matings of 100 (in one case 82) females from the three hybrid lines with *virilis* males were arranged for and the percentages of fertile cultures compared with those from 100 control pair matings of females and males within each of the hybrid lines as well as with the fertility frequency in 100 *virilis* pair matings (Table 1). The left and right columns of the first three lines in the table show that no significant difference between self-fertility of any line and its cross fertility with *virilis* existed. The percentages of fertility for matings involving hybrid Ad and Aoa females are only slightly below those determined for frequency of insemination of pure Ad and Ao females by males of the same strain (96.8 and 97.5 per cent., respectively, Stalker 1942a), and very much higher than the frequencies of interspecific inseminations in these strains as observed by the same author (10.7 and 12.3 per cent.). A further comparison of the

TABLE 1

PERCENTAGE OF FERTILE CULTURES IN PAIR MATINGS OF INDIVIDUALS WITHIN HYBRID LINES, WITHIN THE VIRILIS LINE AND BETWEEN HYBRID FEMALES AND VIRILIS MALES. ALL DETERMINATIONS BASED ON 100 CULTURES EXCEPT IN THE CROSS AOB ♀ × VIR ♂ WHERE 82 CULTURES WERE AVAILABLE

P–♀	Percent of fertile cultures P–♂	
	from hybrid line	from virilis line
Ad	90	93
Aoa	92	94
Aob (exp. 1)	78	78
virilis (exp. 1)	..	91
Aob (exp. 2)	..	87
virilis (exp. 2)	..	83

Matings reported in rows 1–4 were conducted after 30 generations of single pair matings in lines Ad, Aoa and virilis, and after 26 single pair matings in Aob. Matings reported in rows 5 and 6 occurred three generations later.

fertility of crosses involving individuals from hybrid lines with that within the *virilis* line gave no significant differences in the cases of hybrid Ad and Aoa females (90–94 per cent. as compared with 91 per cent. Stalker found 97.7 per cent. of insemination within *virilis* matings). However, both matings involving Aob (table 1, line 3) yielded significantly lower fertility than any of the others. Most of the sterile pairs of the matings Aob × Aob belonged to one or the other of two groups of sibs while the fertility in the remaining pairs, belonging to six groups of sibs was over 90 per cent. as in the other matings. Similarly, fourteen females of the eighteen sterile pairs of the cross Aob × vir belonged to one single group of 25 sibs. It was also found that six of the ten sterile females in the mating Ad × Ad were derived from a single sibship from which seven pairs were set up. These facts show that the sterility found can not be regarded as an intrinsic character of the lines tested but was either due to segregating residual genetic heterogeneity or perhaps rather to unknown environmental circumstances.

In order to test the assumption that the lower fertility in line Aob was incidental, the cross Aob × vir was repeated and a new set of vir × vir matings was arranged as control (Table 1, lines 5 and 6). This time no significant difference in percentage of fertility was observed. The fertility of the outcross approached that of the majority of the earlier lines and surpassed that of the new *virilis* matings. It may be concluded that the frequency of fertile matings between females and males of hybrid origin does not differ from the frequency of fertility in the cross of such females with pure *virilis* males. Thus, all morphological and physiological tests yield the result that the specific differences between *Drosophila virilis* and *D. americana* do not depend on any self-reproducing extra chromosomal elements but on the genetic constitution of the chromosomes of the two species.

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RECOMBINATION AND INTERFERENCE NEAR THE LEFT END OF THE SEX CHROMOSOME OF HABROBRACON[1]

STARTING at the left end of the sex chromosome of *Habrobracon juglandis* (Ashmead), the genes are arranged in the order: speckled (*Sk*, an eye color factor), reduced (*r*, a wing size and vein factor) and glass (*gl*, a structural eye factor). The present experiment was done in order to check recombination and interference in this region, and to compensate for any viability disturbance or position effects by introducing the genes in all possible combinations. In Habrobracon, diploid females produce haploid sons parthenogenetically. Hence, in linkage work, typical testcross ratios are obtained by crossing a female homozygous for each possible gene combination to a complementary male, and breeding the F_1 heterozygous females from this cross as virgins. Throughout this work, all stocks carried the mutant, white eye, as a differentiator for speckled. White is not located on the sex chromosome. The number of possible combinations of *Sk*, *r* and *gl* is limited because *gl* is female sterile and had always to be introduced from the male, and also because *gl is* epistatic to *Sk*.

Table I[2] gives the results of the four possible crosses. In the genotype of the F_1 mother (see col. 2) the gene complement of the parental female is above the line, that of the parental male, below. The non-glass genotypes of the F_2 males (col. 4) were distinguishable, but the glass genotypes (col. 7) could be separated only on the wing character, since speckled does not show in a glass eye. Among the non-glass, the ratios of recombination between *Sk* and *r* (region 1) and between *r* and *gl* (region 2) were computed and appear in column 6 following the singles in the

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[1] The author wishes to acknowledge the assistance and encouragement of Dr. P. W. Whiting and Dr. G. M. McKinley.

[2] Part of these data were included in a University of Pittsburgh dissertation (1942).

given region. Also in this column are the coincidence values following the doubles. Among the glass sons, one of the combined classes contains region 2 recombinations and double recombinations, and hence could be used to determine the ratio of recombination between *r* and *gl*. However no other direct determinations could be made from the glass data.

TABLE I

Exp.	F$_1$ mother	Recomb. Regions	Non-glass F$_2$ males		Ratios of Recomb. & Coincidence	Glass F$_2$ males		Ratios of Recomb.
1	$\frac{Sk}{r\ gl}$	–	Sk	1,977		Sk r gl and r gl	2,048	
		1	+	284	0.106			
		2	r	448	0.167	Sk gl and gl	453	0.179
		1, 2	Sk r	4	0.084			
		Totals		**2,713**			**2,501**	
2	$\frac{Sk\ r}{gl}$	–	Sk r	2,620		Sk gl and gl	3,101	
		1	r	467	0.135			
		2	+	502	0.140	Sk r gl and r gl	494	0.132
		1, 2	Sk	20	0.284			
		Totals		**3,609**			**3,595**	
3	$\overline{Sk\ r\ gl}$	–	+	1,381		Sk r gl and r gl	1,469	
		1	Sk	229	0.127			
		2	Sk r	227	0.125	Sk gl and gl	190	0.113
		1, 2	r	2	0.067			
		Totals		**1,839**			**1,659**	
4a	$\frac{r}{Sk\ \ gl}$	–	r	463		Sk gl and gl	330	
		1	Sk r	44	0.093			
		2	Sk	35	0.077	Sk r gl and r gl	42	0.088
		1, 2	+	7	1.794			
		Totals		**549**			**372**	
4b	$\frac{r}{Sk\ \ gl}$	–	r	1,764		Sk gl and gl	1,490	
		1	Sk r	263	0.126			
		2	Sk	133	0.067	Sk r gl and r gl	183	0.109
		1, 2	+	12	0.654			
		Totals		**2,172**			**1,673**	
	Total count	–		8,205			8,438	
		1		1,287	0.122			
		2		1,345	0.128		1,362	0.139
		1, 2		45	0.264			
		Totals		**10,882**			**9,800**	

The results for crosses 1, 2 and 3 are statistically consistent. In each cross, the non-glass are more numerous than the glass, probably because of better viability and hatchability. The recombination ratios for region 2 based on the non-glass data are reasonably close to those based on the glass data. It is interesting to note that the amount of interference varies markedly with different genic combinations.

The results of cross 4a differ appreciably from those of the previous crosses. The recombination ratios between *Sk* and *r* and between *r* and *gl* are significantly lower than the values obtained in crosses 1, 2 and 3. Moreover, there is a disproportionate number of double recombinations, giving a coincidence value indicative of negative interference; whereas the other crosses showed positive interference. Possible explanations of these differences are: (1) the count in cross 4a is low and hence might not be a representative sample; (2) the double recombination class is type and might therefore be more viable. Several unusual reduced wasps appeared in this cross. In pure stock, reduced shortens the wing and removes that portion of the median vein (Ross system) that runs toward the stigma. Wasps were observed with short wings and some irregularity in the median vein but with the entire vein present.

Cross 4b was run as a check. A sufficiently large number of wasps was counted in order to assure a representative sample. The recombination ratio between *Sk* and *r* agrees with the values obtained in the other crosses, but one of those between *r* and *gl* is significantly different, the one based on the non-glass data; the recombination ratio based on the glass data is consistent with the results of the other crosses. This difference within the cross arises from a deficiency of *Sk*. In this cross, as in 4a, the coincidence value is significantly higher than in crosses 1, 2, and 3. There were 48 wasps with unusual reduced wings. Since this odd expression of the factor, reduced, was not observed in any of the other crosses, it might be ascribed to a position effect of the genes.

Possibly the most representative values for recombination and coincidence in the *Sk, r, gl,* region are obtained by totaling the data. Such a grouping compensates for proportionate disturbances due to viability differences or position effects of the gene combinations involved.

SUMMARY

Sk, *r* and *gl*, three genes marking the left end of the sex chromosome of Habrobracon, are introduced in the four possible combinations. The ratio of recombination between *Sk* and *r* is 0.122; that between *r* and *gl* 0.128. Coincidence is 0.264.

Coincidence varies markedly as the genes are introduced in different combinations.

The recombination ratios obtained in 4a and 4b differ significantly from those obtained in the other three crosses.

Several unusual reduced wasps appeared in crosses 4a and 4b but in no other crosses.

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THE POLYTYPIC SPECIES IN NORTH AMERICAN AMPHIBIANS AND REPTILES

IN Dr. Mayr's recent book[1] there appears a table (p. 124) which lists several geographically restricted animal groups and indicates the percentage of species of each group that are mono-

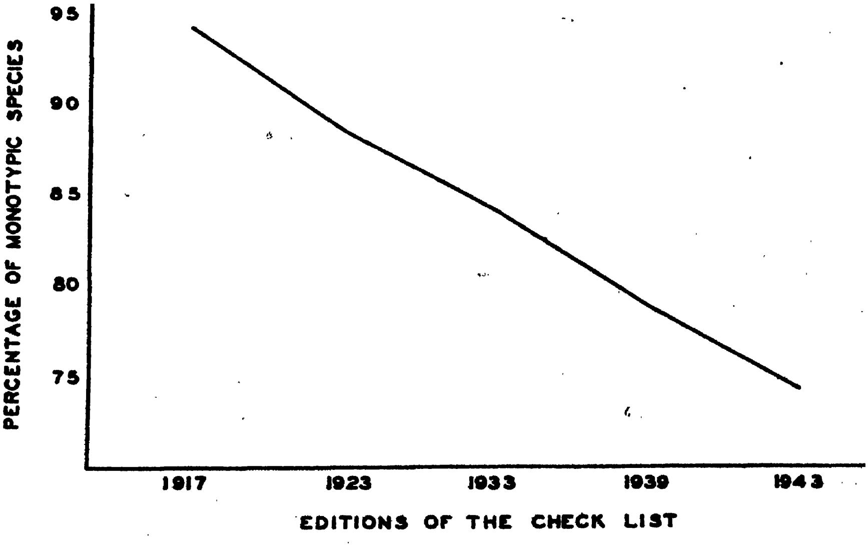

FIG. 1. Graph showing the percentage of monotypic species in succeeding editions of the "Check List of North American Amphibians and Reptiles."

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[1] Ernst Mayr, "Systematics and the Origin of Species." New York, N. Y.: Columbia University Press. Pp. 1–334. 1942.

typic. Dr. Mayr suggests two conclusions to be drawn from this tabulation, the second of which is that "the percentage of monotypic species recorded in a certain group at a given period depends to a considerable extent on the degree of finality which the classification of the respective group has reached." Of the series of groups in his table, two pairs are pertinent in this regard. Miller listed 75.8 per cent. of the species of European mammals as monotypic in 1912, while Ökland regarded only 54.7 per cent. as monotypic in 1937. Hartert considered 37.7 per cent. of the species of Palearctic Passeres monotypic in 1923 and in 1936 reduced the percentage to 29.7.

The "Check List of North American Amphibians and Reptiles," which has been organized through five editions (1917, 1923, 1933, 1939 and 1943) by Leonhard Stejneger and Thomas Barbour, seemed to us to provide ideal material for a tabulation of this nature because it covers the same animal groups within the same geographic area and has been brought together by the same authors several times through a period of years. Fig. 1 summarizes the results of our census of these editions; it includes all the forms listed in each Check List except those that have been introduced into the area.

As the percentage of monotypic species of amphibians and reptiles was reduced from 94.2 to 74.4 the number of genera remained relatively stable (extremes being 121 and 132); the number of species increased slightly from 438 to 500; and the number of subspecies increased sharply from 497 to 751. The average number of forms (species and subspecies) per genus has increased regularly through the five editions from 4.1 in the first edition to 5.7 in the fifth edition and the average number of subspecies per species has increased regularly through the same period from 1.13 to 1.50.

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THE

AMERICAN NATURALIST

VOL. LXXVIII *May–June, 1944* No. 776

DISTRIBUTION OF HETEROCHROMATIN IN THE CHROMOSOMES OF *DROSOPHILA PALLIDIPENNIS*

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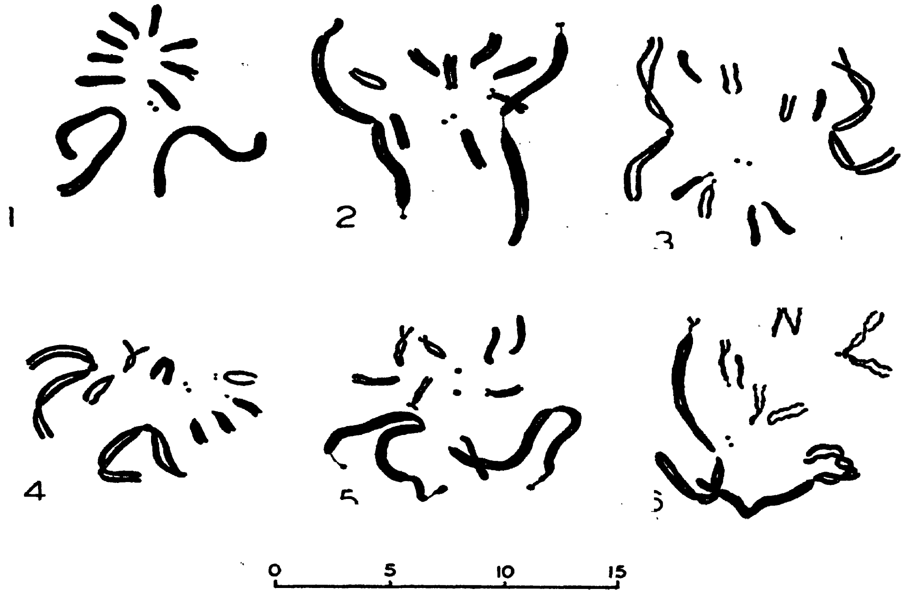
STUDIES on the comparative chromosome morphology in species of Drosophila were initiated by Metz (1914, 1923 and other work) and continued by several other investigators. The excellent work of Wharton (1943) gives semi-diagrammatic drawings and descriptions of metaphase chromosome groups in 86 species of Drosophila, together with statements as to the number of chromosome strands found in the salivary gland cells of all these species. The information available permits certain conclusions to be drawn and certain new problems to be formulated regarding the kinds of evolutionary changes in the chromosome structures that have taken place in the phylogeny of this genus. The commonest type of change is inversion of chromosome sections which do not include the locus of the centromere. This could be expected on theoretical grounds, since heterozygosis for such inversions as a rule causes no reduction of the fertility of the flies. The next most frequent type of change seem to be translocations which lead to junction or separation of whole chromosome arms, from the centromere to the free end. Data on the fertility of translocation heterozygotes of this sort are not available and are urgently needed. Inversions of chromosome sections including the centromeres are less common than other changes; translocations which entail exchanges of parts of chromosome arms are rare, although they undoubtedly do occur. This is because heterozygosis for such inversions and translocations does, judging from examples induced in laboratories chiefly by means of x-ray, reduce the fertility of the flies to a considerable extent; such changes should be discriminated against by natural selection from the time they appear in the populations until they become so frequent that many inversion and translocation homozygotes are produced. The fact that chromosome changes which are supposed to be temporarily deleterious to their carriers may nevertheless become established in some natural populations is very important, since it suggests that under certain circumstances evolutionary alterations may take place notwithstanding the counteraction of natural selection. Because of this, the field of comparative chromosome morphology of Drosophila can not be regarded as exhausted. It would seem, however, that from now on a somewhat more detailed sort of study of at least some selected species ought to be undertaken, to include careful comparisons of the morphology of somatic metaphase chromosomes as well as of the corresponding prophases with the salivary gland chromosome structures. The distribution of the euchromatic and heterochromatic sections in chromosomes and differences in the phyletic behavior of these diverging types of chromosomal materials have been somewhat neglected, although they might shed new light on some important issues.

This article is devoted to a description of the chromosomes of *Drosophila pallidipennis* Dobzhansky and Pavan, which show several interesting and unusual characteristics. *D. pallidipennis* is a species so far known from only a single locality, Furnas, near Iporanga, state of São Paulo, Brazil. It is apparently related to *D. hyalipennis* Duda, described from a single museum specimen from Cuzco, Peru. Both species have a pair of so-called prescutellar bristles, which places them in Duda's subgenus or genus Paradrosophila. Paradrosophila is, however, not a natural group, and the species under discussion should be placed in the genus and subgenus Drosophila s. str., within which they do not however show clear affinities to any other known species groups.

METAPHASE CHROMOSOMES

Metaphases in the giant nerve cells (neuroblasts) of larval ganglia have been examined in acetic orcein and acetic carmine smear preparations. In either sex, the chromosome complement consists of twelve chromosomes, including four pairs of rods, a pair of very large V's and a pair of small dots (Figs. 1–5). In most cells, one of the rod-like pairs is distinguishable from the other three by a slightly greater length. Among the shorter rods, one pair shows in some cells small satellites well separated from the body of the chromosome (Figs. 2–5). This chromosome probably has a subterminal centromere, while in the other rods the centromere appears to be terminal. The dot-like chromosomes are so small that in many cells they can not be identified. The V-shaped elements, which are the X- and Y-chromosomes, are relatively enor-



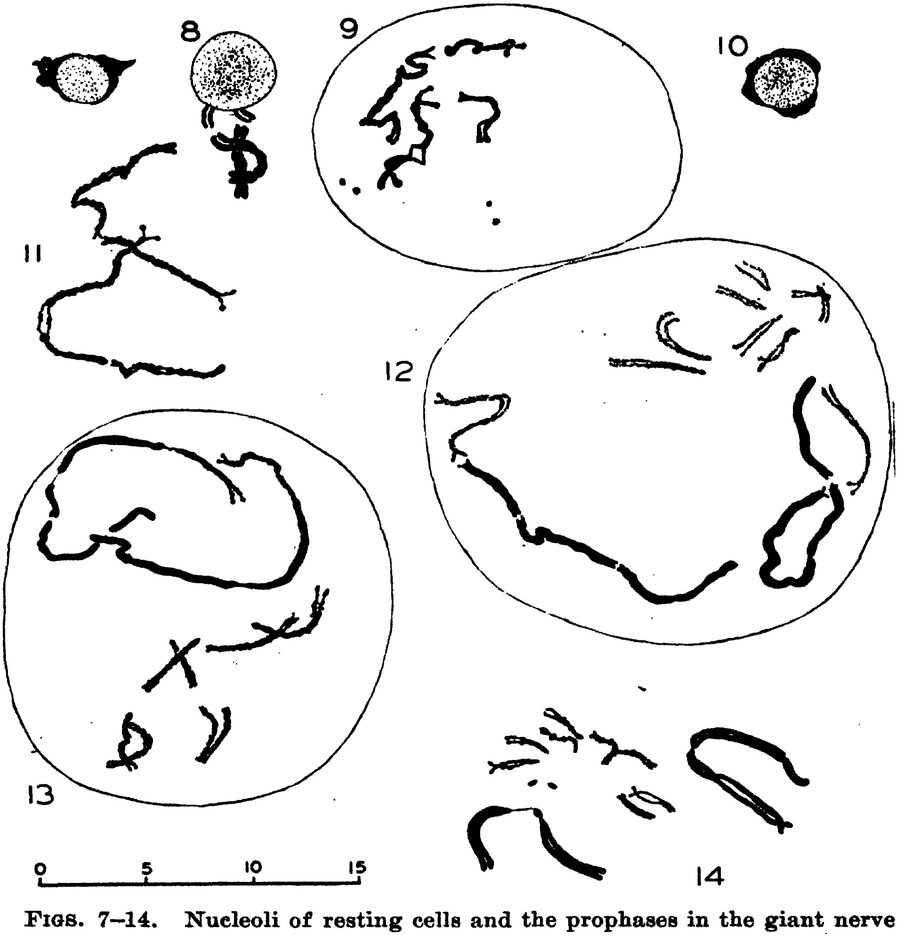
FIGS. 1–6. Metaphases and prometaphases in the giant nerve cells of larval ganglia of *Drosophila pallidipennis*. The scale represents 15 micra.

mous. The V's are not equal-armed; the length of the longer arm is approximately equal to the combined lengths of three rod-like chromosomes in the same cell, while the shorter arm is between two and three times longer than the shorter rods. Thus, one of the chromosomes is in the species under discussion longer than all other chromosomes of the haploid set combined. Although great size differences between chromosomes of a species are a common phenomenon, a difference so striking as observed here is not, to the writer's knowledge, encountered in any other animal or plant species. In some cells, especially at pre-metaphase, one or both arms of the V-shaped chromosomes show fairly large terminal satellites (Figs. 2 and 5). The equational splits in the chromosomes are very clearly visible; in fact, in some cells the equational halves of some of the rod-shaped elements lie so far apart that the connection between them at the centromere is invisible (Fig. 3). Such half-chromosomes can be distinguished from whole chromosomes by their smaller thickness. In the V-shaped chromosomes, a secondary constriction close to the centromere is sometimes visible in the shorter arm (Figs. 3 and 4).

Owing to the striking differences in size between the chromosomes, their relative positions in metaphase plates are interesting. The center of the plate is usually occupied by the small dots, with the rods arranged in a circle or a semicircle around them. The large V's lie either next to each other on one side of the plate (Figs. 1, 4, 5) or opposite each other (Figs. 2 and 3). In no cells was one of the V's seen lying inside the other, as V-shaped chromosomes of Drosophila usually do on account of the somatic pairing. The somatic pairing is weak in giant nerve cells, but the smaller brain cells, which have a pronounced somatic pairing, show the same distribution of the chromosomes in metaphase plates as do the large cells.

MITOTIC PROPHASES

The interkinetic nuclei contain a nucleolus, which, in acetic orcein and carmine preparations, appears as an irregular sphere with a dark outer envelope and a distinctly lighter core (Fig. 10). Some nucleoli show the outer envelope to consist of strongly staining and irregularly convoluted strands (Fig. 7). It is possible that the condition represented in Fig. 7 must be regarded as the



FIGS. 7–14. Nucleoli of resting cells and the prophases in the giant nerve cells of larval ganglia of *Drosophila pallidipennis*. The scale represents 15 micra. The nuclear membrane is omitted in Figs. 7, 8, 10, 11 and 14.

first sign of the onset of prophase. In any case, this condition is met with less frequently than that shown in Fig. 10. The chromatic portion of the nucleolus consists of parts of X- and Y-chromosomes. The association of nucleoli in resting cells with heterochromatic portions of chromosomes has been described in several species of Drosophila by Heitz (1933a, b), Kaufmann (1934) and others. In *D. pseudoobscura* the nucleolus has one or two satellites around which the condensation of the X- and Y-chromosomes begins (Dobzhansky, 1934). Among the species with which the writer is familiar, *D. pallidipennis* has the largest chromosomal component in the nucleolus.

At the beginning of the prophase, the light core of the nucleolus (the nucleolus proper) becomes separated from the chromosomal parts, which increase in size and begin to show the equational splits (Fig. 8). Immediately thereafter the nucleolus disappears from view. Stages like that shown in Fig. 8 are seen rather seldom. The heterochromosomes rapidly elongate, and the nuclear cavity shows irregularly twisted, intensely chromatic strands with varying numbers of constrictions so strong that the chromosomes appear broken into fragments (Fig. 9). Some of these constrictions probably mark the loci of the centromeres and others the nucleolus organizers, but the writer has not succeeded in distinguishing them. One or two pairs of small chromatic dots may be seen in some, but by no means in all, nuclei (Fig. 9). These dots possibly represent the pair of dot-like autosomes and the satellites of one of the rod-shaped pairs (see above), but this is not certain. The heterochromosomes elongate further and become thinner, leading to a very interesting stage at which the nucleus contains two very long chromosomes with irregular outlines and not a trace of any other chromosomes, except for the above-mentioned small dots (Fig. 11; in this and in Figs. 7, 8 and 10 the nuclear membrane is omitted). A careful examination usually discloses that the irregularity of the outlines is caused by the chromosome strands being composed of alternating thicker and more slender parts, which must be described as chromomeres. This is especially clear in those portions of the chromosomes in which the equational halves diverge more widely. It is, however, not possible to count these chromomeres. The constrictions are sometimes more and sometimes less clearly pronounced. The ends of the chromosomes are sometimes elongated to form small pycnotic bulbs, or else are split into paired satellite-like structures (Fig. 11). The precocious nucleination of the heterochromatic portions of chromosomes compared to the euchromatic ones has been described in other species of Drosophila (see Heitz and Kaufmann, *l.c.*), but nowhere is the difference as great as in *D. pallidipennis,* where the heterochromatin is clearly visible while no trace of the euchromatic chromosomes has appeared.

Progressive nucleination of the heterochromatic portions of the X- and Y-chromosomes leads to disappearance of the chromomeric structure and of the irregularity of the outlines (Fig. 12). At the same time there appear very faintly staining euchromatic strands. In favorable cells the number of these euchromatic strands may be counted as nine or ten (Fig. 12). Eight of them are obviously the rod-shaped autosomes, with the equational splits as a rule very clearly visible. One or two of the euchromatic strands are the euchromatic portions of the X-chromosomes. Only one limb of the X has a euchromatic portion, the other limb is entirely heterochromatic. Although the euchromatic and the heterochromatic portions of the X-chromosomes are separated by a large non-staining gap (a secondary constriction), the continuity between them may be clearly indicated (the X-chromosome on the left in Fig. 12). But frequently the gap is so wide that the connection between the two portions can only be inferred (the X-chromosome on the right in the same figure). The gap-like constrictions in the heterochromatic portions continue to be visible, but their number is variable, even in the two chromosomes in the same nucleus. Since, even in the smear preparations, the chromosomes at this stage lie in three dimensions, it is difficult to make exact comparisons of the relative lengths of the euchromatic and heterochromatic portions. The euchromatic parts of the X-chromosomes are clearly much shorter than their heterochromatic ones, and usually appear to be as long as or longer than any of the autosomes. The total length of the heterochromatic segments is about equal to, and in any case not much shorter than, the total length of all the euchromatic segments. Furthermore, the heterochromatin, as clearly seen in the figures, is concentrated entirely in the X- and Y-chromosomes, with the possible exception of the small dots and of the centromere ends of one of the autosomes, which can be discerned in some nuclei but not in others. Both the large amount of heterochromatin and its complete or nearly complete restriction to the X- and Y-chromosomes set *D. pallidipennis* apart from any of its congeners studied in this respect. The X- and the Y-chromosome may be distinguished because the latter has no euchromatic section. However, the large gaps that frequently exist between the hetero- and euchromatic sections of the X make it easily confused with a Y-chromosome.

The progress of the prophase leads to a nucleination of the euchromatic chromosomes and sections, which now stain only a little less than the heterochromatic sections of the X and Y, but can be distinguished from the latter by uneven outlines and chromomere-like composition (Fig. 13). Cells of this kind are common and frequently admirably clear. Measurements of the chromosome length are still difficult, but it often appears that at this stage the combined length of the euchromatic portions is somewhat, although not much, greater than that of the heterochromatic ones. Equational splits usually disappear in the heterochromatin, but remain visible in the euchromatin. The chromosomes gradually begin to arrange themselves in an equatorial plate, and it is at this stage that an interesting detail presents itself (Figs. 14 and 6). The euchromatic section of the X-chromosome, which is, of course, attached to the heterochromatic portion, loses its chromomeric structure before the euchromatic chromosomes do so. In some cells the differentiation of the X into hetero- and euchromatin becomes obliterated; in others (Figs. 14 and 5), the euchromatic sections fail to show the equational split which by now is clear in the heterochromatin. Thus, the rate of nucleination of the euchromatic sections seems to depend on the proximity to the heterochromatic ones. By the time pro-metaphase and metaphase are reached, the distinction between hetero- and euchromatin is eliminated entirely (Figs. 1 to 5).

SALIVARY GLAND CHROMOSOMES

Drosophila pallidipennis is excellent material for studies on salivary gland chromosomes. Acetic orcein preparations have been studied. The cells show five chromosome strands each, the terminal and the basal portions of which are shown in Fig. 15 (composite drawings from several cells). Compared to other species of Drosophila, some unusual traits are observable. First of all, a chromocenter uniting the bases of all chromosomes is seldom formed (only two cells with perfect chromocentra from which all five chromosomes radiate have been seen). As a rule, some or all autosomal strands lie free in the nucleus without contact with a very large chromocentral mass. That mass is an integral part of the X-chromosome, which very frequently lies separate in the nucleus with no other chromosome attached (Figs. 15 and 18). The X-chromosome is clearly distinguishable from the autosomes because it is pale and somewhat thinner in male larvae (Fig. 17). Two, three or all four autosomes are frequently associated by their bases (Fig. 16), and one to four autosomes may have their bases in contact with the heterochromatin of the X. It is not possible to decide whether the lack of a regular association of the bases of all chromosomes obtains in living cells or is an artifact produced by the pressure of the cover slip in smearing. Bauer (1936a) has shown that in species of Drosophila with a normal chromocenter, the pressure of the cover slip may break the chromocenter into sections belonging to individual chromosomes, the contact between one or two euchromatic arms joined to a given portion of the chromocenter being usually preserved. In any case, the association between the bases of the autosomes and the chromocentral mass which wholly belongs to the X-chromosome is weaker in *D. pallidipennis* than in any other Drosophila species with which the writer is familiar. It must be remembered that in some Diptera other than Drosophila no chromocenter is formed (Metz, 1935, Bauer, 1936, and others).

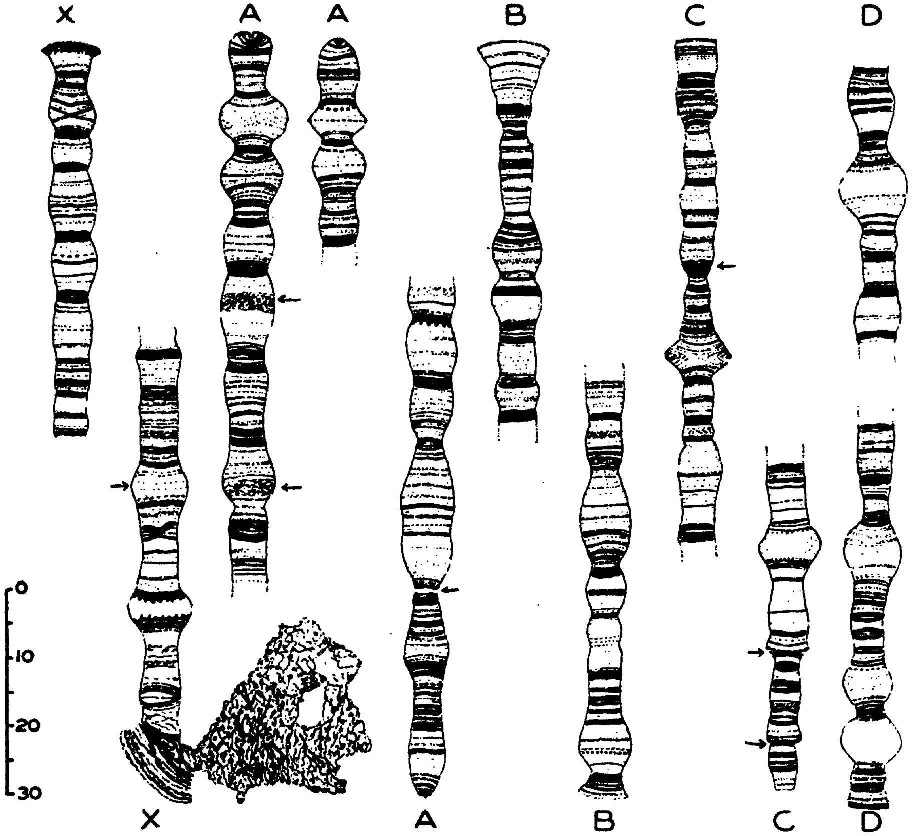


Fig. 15. The distal and proximal parts of the salivary gland chromosomes of *Drosophila pallidipennis*. The scale represents 30 micra.

Examination of the basal portions of the autosomes fails to disclose in them the presence of much material which looks like heterochromatin. This is especially well visible in cells in which the bases of all four autosomes are associated (Fig. 16). Such cells usually show a small heterochromatic mass which, however, is not obviously associated with any particular chromosome (on the right in Fig. 16); while the bases of the autosomes end in some anastomosing strands which unite the bases with each other and with the small heterochromatic mass. Where that mass comes from is unclear; the most probable guess is that it corresponds to the dot-like autosomes. If so, the latter are composed mostly of heterochromatin. Under these circumstances it is not clear what brings the bases of the autosomes together with one another or with the chromocenter in some cells. We must postulate either a special force, or else the presence of some heterochromatic discs at bases of the autosomes which attract each other, in a manner perhaps analogous to the attraction of the free ends of the chromosomes described by Hinton and Atwood (1941) in *D. melanogaster* and *pseudoobscura*. The free ends of the chromosomes in these species also fail to show clearly heterochromatic discs, and yet they do attract each other. It may be noted that the free chromosome ends in *pallidipennis,* with the exception of the X-chromosome (see below), rather seldom show associations.

The chromosomes are, of course, easily distinguishable by their disc patterns. The longest autosome, labeled A chromosome, has an acuminate free end followed by two inflated bulbs (Fig. 15). The terminal discs are bent inwards to form a funnel-shaped figure (a more and a less extreme expression of this condition are represented side by side in Fig. 15). The same structure of a chromosome end has been described by Bauer (1936a) in a chromosome of *D. hydei,* but whether the chromosomes of the two species are homologous is open to question. Two rather short regions in the distal portion and one in the proximal portion of the A-chromosome (denoted by arrows in Fig. 15) look, in some cells at least, like typical heterochromatin, which is so conspicuously absent at the base of this chromosome. The subbasal heterochromatic section is a "weak place" where the chromosome is constricted and very frequently broken, while the distal sections, on the contrary, tend to flair up and to form inflated bulbs.

Another autosome, B-chromosome, has its free end broadened to various extents in different cells—a condition precisely opposite to that of the free end of A-chromosome. The base of B is also broadened, and in some cells approaches the condition which may be described as intermediate between eu- and heterochromatin. C- and D-chromosomes (autosomes) have more or less cylindrical free ends. In the subterminal portion of C there is a section (marked by an arrow in Fig. 15) which is as typi-

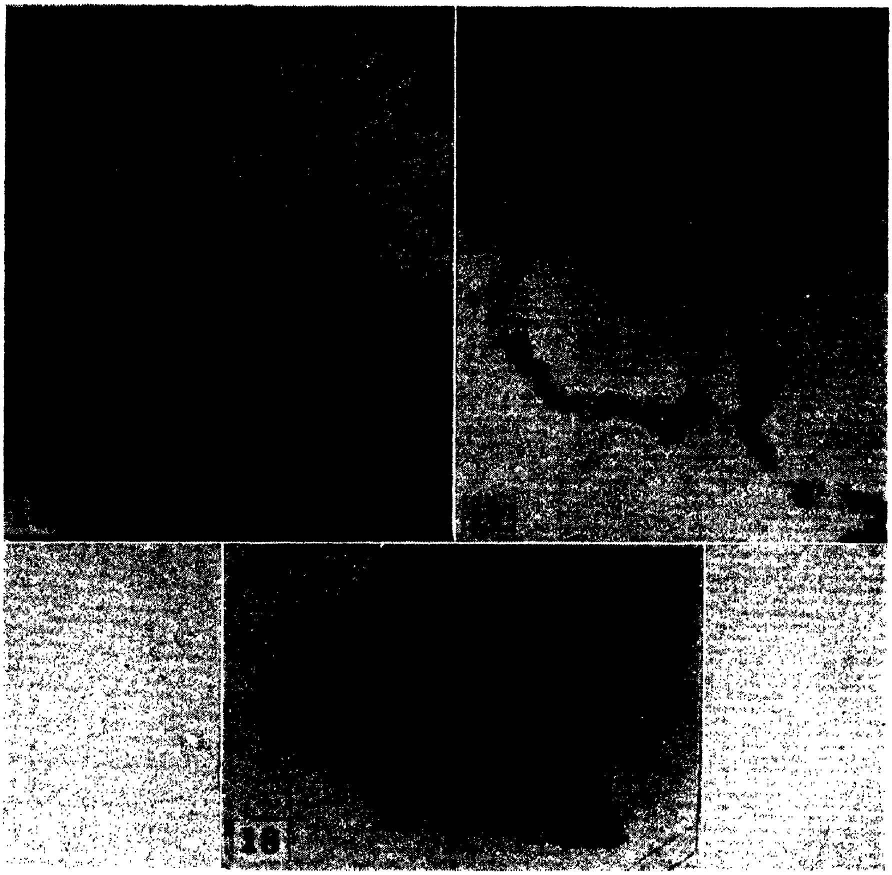


FIG. 16. The basal parts of the autosomes in the salivary gland cells of *Drosophila pallidipennis*. FIGS. 17 and 18. The basal portion of the X-chromosome and the chromocenter in a male (Fig. 17) and a female (Fig. 18).

cally heterochromatic as is the chromocenter at the base of the X. Close to the base of C there are two "weak spots" also bounded by what looks like a few heterochromatic discs (arrows in Fig. 15). The short segment of C lying between the base and the most basal "weak spot" is, curiously enough, much thinner in most cells than the rest of the chromosome (this condition is clearly visible in the photograph in Fig. 16). Proximally from the subterminal heterochromatic section, C-chromosome has a bulb which shows in most in most cells a typical "repeat pairing" of the constituent discs; in some cells this condition is diagrammatically clear. The relatively short D-chromosome has, as its distinguishing features, large bulbous inflations at the base and in the subterminal portion.

The X-chromosome is most interesting. The first attempts to draw the disc pattern of its basal portion produced quite divergent drawings. The difficulty proved to be twofold. First, the basal one third to one half of this chromosome contains at least three heterochromatic portions of so considerable an extent that in many cells they are attracted to each other and to the chromocentral mass, and cause the chromosome to be broken and irregularly convoluted (Fig. 17). Second, the limits between hetero- and euchromatin in this chromosome vary so much from cell to cell that a fairly long basal section may in some cells consist of apparently euchromatic discs, while in other cells parts of the same section are included into the chromocentral mass and are no longer identifiable. The base of the X drawn in Fig. 15 is close to the extreme "euchromatic" end of the variation range. Next to the foamy-looking chromocenter proper (comp. Fig. 18) lies a large block of material intermediate between hetero- and euchromatin, which probably represents a large duplication area ("repeat"). This is followed by a short diffuse section, by another small mirror-image duplication, another diffuse section, a "bulb" with some heavily staining discs, a fairly large euchromatic section with two "bulbs" and a large typically heterochromatic section (not shown in the part drawn in Fig. 15). The photographs (Figs. 17 and 18) also show the basal portions of the X in two different cells (Fig. 17 from a male and Fig. 18 from a female larva). In Fig. 17 three interstitial heterochromatic sections can be seen, two of which are associated with each other and one with the basal chromocentral mass. In Fig. 18 the part of the chromosome lying between the most basal of the interstitial heterochromatic sections and the chromocenter can be seen. A comparison of this part of the chromosome in Figs. 17 and 18 is instructive. The arrows in both figures point at a bulb, which is also marked by an arrow in Fig. 15. In Fig. 18 this bulb is heterochromatin-like and sends a few slender strands to the chromocenter. In Fig. 17 only a short euchromatic section is found between this bulb and the chromocenter. In Fig. 18 the same euchromatic section is seen strongly condensed, but beyond it lies another bulb bounded with heavy discs (compare Fig. 15) and a short apparently euchromatic section which joins the block of the semi-heterochromatic material which probably represents a repeat area (see above). There is, consequently, a fairly large section with discrete discs in Fig. 18 which is included into the chromocenter in Fig. 17. In some cells all of the material up to the heavy discs preceding the bulb marked with arrows in Figs. 15, 17 and 18 is heterochromatic and fails to show discrete discs.

These striking variations in the position of the boundary between the hetero- and euchromatin in the base of the X-chromosome may be compared with the observations of Schultz (1939), who claimed that discs normally lying in the euchromatin change their stainabilities when transferred by chromosomal aberration to the proximity of the heterochromatic chromocenter;[4] in extreme cases these discs disappear entirely. Their loss is used by Schultz to explain certain phenomena of mosaicism in *Drosophila melanogaster.* These observations have been contested by Sutton (1940), according to whom the euchromatic discs transferred close to the chromocenter retain as a rule their normal properties. The conditions found in the X of *D. pallidipennis* show incontrovertibly that the boundary between the hetero- and euchromatic parts of the chromosome fluctuates so much that many discs which appear euchromatic in some cells are "heterochromatized," become included into the chromocenter, and are no longer identifiable as discrete discs in other cells. There is, however, no need either in this case or in *D. melanogaster* mosaics, to suppose that the genetic materials contained in any of these discs undergo a physical loss. The disappearance of a disc from view may be perfectly well accounted for by Bauer's (1936a, b) hypothesis of the disarrangement of chromomeres in the hetero- compared to the euchromatic regions. This hypothesis is compatible with the assumption made by Schultz (*l.c.*) that the functioning of the genes contained in the chromomeres is altered when the latter are "heterochromatized." This assumption, in turn, necessitates another one, namely, that variable "heterochromatinization" takes place not only in salivary gland cells but in other body cells as well. Direct evidence on this is lacking. Perhaps the observations described above, that the euchromatic portions of the X-chromosome become nucleinated earlier during the mitotic prophase than the euchromatic autosomes, is relevant. The obvious difference between the euchromatic part of the X and the autosomes is that the former has a physical continuity with a large mass of heterochromatin and the latter do not.

The interstitial heterochromatic sections are so large and numerous in the X-chromosome that only its terminal one third may be described as truly euchromatic. Its free end (Fig. 15) shows, however, a structure again resembling heterochromatin. Patterson, Stone and Griffen (1940) draw a rather similar structure in the free end of the X-chromosome of *D. virilis* and Wharton (1942) in *repleta*. Whether this indicates a homology of the free ends of the X-chromosomes in the three species is uncertain. Similar structures of free ends of chromosomes have also been described in some species of Sciara and Chironomus. In female cells the two X-chromosomes contribute equally to the formation of the huge chromocenter. Two cells have been found in which the X's were accidentally not paired for some distance from the base, and the bases were attached each to a separate half-chromocenter. Since the X- and Y-chromosomes are about equal in size at metaphase, and since the whole Y is heterochromatic, the chromocenter in male larvae must be formed about equally by the X and the Y. Therefore, cells might be found in which the portions of the chromocenter formed by the X and the Y are not fused; such cells have not been found.

The following table shows the relative lengths of the euchromatic parts of the chromosomes, as seen in the salivary gland cells, in percentages of the total length of all the chromosomes in a given nucleus. The data are obtained by measuring the chromosomes with the aid of a measuring wheel in camera lucida drawings of 25 cells selected for having all the chromosomes reasonably well straightened out. The mean values and their standard errors are given.

Chromosome	M ± m
X	18.36 ± 0.47
A	25.60 ± 0.64
B	19.04 ± 0.34
C	21.20 ± 0.65
D	15.76 ± 0.43

A-chromosome is the longest and D is the shortest; the three other chromosomes are about equal in length. The X may be somewhat longer than the data indicate; on account of its interstitial heterochromatic sections the X is seldom as well straightened out as the other chromosomes.

DISCUSSION

The relative amounts of hetero- and euchromatin differ in different species of Drosophila. According to

Sirotina (1938), *D. busckii* has a very large nucleolus but no chromocenter in its salivary gland cells. Nevertheless, the bases of the chromosomes tend to be associated together in this species, as they do in species with clear chromocentra. Since Sirotina has not studied the mitotic prophases, it is possible that in *D. busckii* the chromosomes have heterochromatic parts which do not assume in the salivary gland cell the foamy appearance of a normal chromocenter. The drawings of Heitz (1933a, 1935) show that in *D. virilis* a little less than half of the prophase length of each chromosome is heterochromatin, and yet the chromocenter in this species is small and compact (Heitz, 1934; Patterson, Stone and Griffen, 1940). In *D. melanogaster* only about a fifth or sixth of the prophase chromosome length is heterochromatic (not counting the totally heterochromatic Y-chromosome), but this species has a fairly large chromocenter (Heitz, 1933b; Kaufmann, 1934). *D. pallidipennis* has about half of the total chromosome length heterochromatic, and an enormous chromocenter is formed.

The distribution of the heterochromatic material among the chromosomes is also variable from species to species. The situation which apparently can be regarded as typical (phylogenetically primitive?) for the genus Drosophila is equal apportionment of the heterochromatin among all the chromosomes, except the small dot-like pair and the Y-chromosome, and its concentration chiefly or exclusively near the centromeres. As stated above, the chromosomes of *D. virilis* have each about one half of the length composed of heterochromatin, and they contribute about equally to the formation of the chromocenter in the salivary gland cells. In *D. melanogaster* and *D. simulans* about one third of the X and one sixth or less of each autosomal limb is heterochromatic; the X and the two V-shaped autosomes (corresponding to four limbs) contribute about equally to the formation of the chromocenter. In *D. pseudoobscura,* the X-chromosome is V-shaped, with one of its limbs approximately corresponding to the X and the other limb to one of the autosomes of species with a rod-like X; the former limb has considerably more heterochromatin than the latter. Two of the autosomes have each approximately as much heterochromatin as the limb of the X with least heterochromatin, while the third autosome is almost entirely euchromatic; the dot-like autosome is mostly euchromatic (Bauer, 1936, and observations of the writer). Seven types of Y-chromosomes, all of them completely heterochromatic but some more than twice as long as others, are known in different strains of this species. *D. prosaltans* and *D. sturtevanti* have, in their salivary gland cells, about three quarters of the heterochromatin concentrated in two autosomal limbs, while another autosome and the two X-chromosome limbs contain the remaining one quarter (Dobzhansky and Pavan, 1944). The mitotic prophases in these species have not been examined. *D. ananassae* has distributed its heterochromatin still differently: a large part of it became translocated onto what corresponds to the small dot-like autosome in other species of Drosophila, making the latter fairly large at mitosis, while the four autosomal limbs and the X-chromosome each contain a small heterochromatic area (Kaufmann, 1937).

Concentration of the heterochromatin predominantly in a single chromosome is known in some species. *Drosophila hydei* has a V-shaped X-chromosome, one whole limb of which is heterochromatic, while the other limb has a small heterochromatic section at the centromere. The four rod-like autosomes seem to be entirely euchromatic in prophases, or else have only very small heterochromatic sections near the centromeres (Heitz, 1933b). Wholly heterochromatic limbs of V-shaped chromosomes are not rare. Comparing the metaphase chromosome patterns with the corresponding salivaries, Wharton (1943) found heterochromatic chromosome limbs in *D. melanopalpa, fuliginea, mercatorum, hydei, parachrogaster* and *subbadia.* In some other species a rod-like chromosome which is fairly long at metaphase is represented in the salivaries by a small euchromatic section, evidently because most of its metaphase length is due to heterochromatin. *D. funebris* has five pairs of rod-like chromosomes, one of which, the X, is considerably longer than any of the others. Heitz (1933a) found that about one half of the X is heterochromatic, while the autosomes have only very small heterochromatic sections near the centromeres. In *D. pallidipennis* the amount as well as the distribution of the heterochromatin is unusual. Except for the few interstitial heterochromatic sections in the autosomes, the whole heterochromatin is concentrated in the enormous X- and Y-chromosomes. The centromere ends of the autosomes have few or no heterochromatic discs.

Two mechanisms could bring about the differences in the distribution of heterochromatin among the species of Drosophila. First, heterochromatin may be shifted from chromosome to chromosome by translocations. Second, the amount of heterochromatin within a chromosome may be modified by duplications and deficiencies. Deficiencies take place only rarely in the phylogeny of euchromatic sections, because they affect adversely the viability of homozygotes. But, judging from the relatively little effect produced by losses of heterochromatic Y-chromosomes, it is the quantity rather than the quality of heterochromatin that is important. However, too much reliance should not be placed on the above argument: the heterochromatic sections of chromosomes other than the Y may not be "inert" and may be qualitatively differentiated. If so, the loss of a certain heterochromatic section can not be compensated by reduplication of another section. The similarity of the X- and Y-chromosomes in *D. pallidipennis* suggests that their heterochromatic sections have a common origin, and have been shifted from the Y to the X, or *vice versa,* by crossing-over or translocations. Whether or not both of them had arisen by summation of the heterochromatic sections located in the autosomes of other species of Drosophila is an open question.

Concentration of heterochromatin close to the centromeres is certainly the rule in Drosophila species, although

Kaufmann (1939) and Prokofyeva-Belgovskaya (1939) have presented evidence that some interstitial sections having certain properties of heterochromatin exist in *D. melanogaster*. Concentration of the heterochromatin near the centromeres must, for some reason, be advantageous; this is attested by the fact that none of the rather numerous inversions found in natural populations of Drosophila species involve breaks in the proximal heterochromatic sections, although such breaks are quite common among the x-ray induced chromosomal aberrations. Yet, the rule has exceptions: most of the "euchromatic" part of the X-chromosome of *D. pallidipennis* is really a mixture of hetero- and euchromatic sections. If, as Schultz (1939) believes, transposition of genes normally lying in euchromatin to the vicinity of heterochromatin results in position effects and mosaicism, such transpositions are likely to be discriminated against in natural populations. *D. pallidipennis* shows, however, that the genetic variations so produced need not always be harmful. It should be recalled in this connection that in Chironomus, Sciara and other dipterous genera heterochromatic sections are not necessarily concentrated in any particular portions of the chromosomes (Bauer, 1936b; Poulson and Metz, 1938, and others). Further studies are necessary to clarify these apparently contradictory findings.

SUMMARY

The chromosomes of *Drosophila pallidipennis* are exceptional in several respects. One of its six chromosome pairs is longer at metaphase than all other chromosomes combined. The large chromosomes are X- and Y-chromosomes, they consist chiefly of heterochromatin, and at mitotic prophases they condense long before the euchromatic autosomes and the euchromatic part of the X become visible. In the salivary gland cells, the autosomes (except the small dot-like pair) show no obvious heterochromatin at the centromeres, but some interstitial heterochromatic sections are present. Several fairly

large interstitial heterochromatic sections occur also within the predominantly euchromatic part of the X-chromosome. The boundary between the hetero- and euchromatic sections of the X is variable: many discs that appear euchromatic in some cells are heterochromatic in other cells.

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PHYSIOLOGICAL EFFECTS OF GENES: THE FLIGHT OF DROSOPHILA CONSIDERED IN RELATION TO GENE MUTATIONS

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THE negative survival value of mutant individuals in nature frequently seems much larger than can be accounted for in terms of the obvious morphological differences between the mutant and wild animals. This has led to the rational assumption that single gene mutations generally produce manifold effects. From this point of view, a morphological character differentiating a mutant from the normal wild animal can be neutral in itself and yet the mutation may possess definite survival value as a result of its additional morphological and physiological effects.

An increasing amount of evidence, recently reviewed by Dobzhansky (1941) and Dobzhansky and Holz (1943), has been obtained in support of this theory. For example, it is well established that mutations in Drosophila frequently affect the shape of the spermatheca. It is also generally agreed that mutant animals often show altered and, for the most part, decreased viability (see Dobzhansky, 1941).

Since manifold effects of a physiological nature have an especially direct bearing on the well-being and adaptation of the animal, physiological effects such as those concerning viability are of particular interest. Yet due to the difficulties inherent in quantitative studies of physiological characters, data of this sort are still meager and have generally been difficult to obtain.

In a previous investigation (Reed, Williams and Chadwick, 1942) the frequency of wing-beat during flight was studied on a large number of species and races of Drosophila: under standardized experimental conditions each species and race was found to be characterized by a narrow range of wing-beat frequencies. It was therefore possible to separate the various species in terms of this physiological character. Such measurements when performed on suitable hybrid individuals demonstrated that the inheritance and magnitude of wing-beat frequency are conditioned by a multiplicity of genes. This conclusion may seem almost self-evident since the flight physiology involves either directly or indirectly the majority of the physiological and morphological systems of the insect.

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From this résumé it is clear that an examination of the frequency of wing-beat of mutant strains should yield some information in regard to the effects on flight of the mutant genes in question. Such an analysis should ideally be performed on mutant strains that differ from the wild "control" strain by a single gene (see Dobzhansky and Holz, 1943), but in practice this objective is very difficult to attain with certainty. In the present report the wing-beat frequencies of an extensive series of approximately isogenic strains of *Drosophila melanogaster* have been catalogued and compared with that of the wild strain from which the former were derived.

MATERIAL AND METHODS

The measurements of wing-beat frequency were performed stroboscopically by means of the technique described by Williams and Chadwick (1943). The animals were fastened to a support and the frequency of wing-beat determined during short flights stimulated at twenty-second intervals by removal of a platform from under the animal's feet. Fifteen measurements were generally made on each individual. All experiments were carried out at 20.0 ± 0.1° C. on virgin female animals 72 ± 2 hours old. The insects were the offspring of single pair matings and were raised under uniform food conditions in a room having a constant temperature of 20.0 ± 0.5° C.

All the stocks of this experiment have the same genetic background. For some years a wild-type stock has been maintained exclusively by brother-sister inbreeding with a single pair as the parents of each subsequent generation. At the time the animals were tested this strain had reached the 122nd generation of such inbreeding. During the course of this process the strain has undoubtedly changed because of the fixation of new mutations; however, since each generation comes from only two individuals, new mutations must either become fixed or eliminated quite rapidly due to the extremely small effective population size. This method is not as satisfactory for the second and third chromosome as the balancer method; over a long period of time, however, one would expect little difference in the results, unless, due to the continuous occurrence of new small mutations, the balancing is repeated at regular intervals.

Preparations for the present experiment were begun by backcrossing various laboratory mutant strains to the highly inbred wild stock, as indicated in the following diagram. Each generation was derived from a single pair of animals.

1. ♂ mutant	X	♀ wild
2. ♀ heterozygote (from 1)	X	♂ wild
3. ♂ mutant (from 2)	X	♀ wild
4. ♀ heterozygote (from 3)	X	♂ wild
etc.		

This process was continued for an average of 24 backcrossing generations in order to eliminate the chromosomes derived from the mutant, with the exception of the chromosome containing the mutant gene under consideration. This procedure also served, via crossing-over in alternate generations, to replace all save a short segment of the mutant chromosome with that of the wild strain. Thus the mutant gene to be studied, along with a few closely adjacent genes, was, in effect, introduced into the original wild strain.

Dobzhansky and Holz (1943) have subsequently demonstrated a better method for obtaining isogenism; namely, by x-raying the homozygous wild strain and producing the mutations *de novo*. A small number of mutations produced by this method have been studied and will serve as a check on the larger group of approximately isogenic strains established by backcrossing.

WING-BEAT FREQUENCY OF THE WILD "CONTROL" STRAIN

Since the effects of the mutant genes upon flight were determined in most cases by a comparison of the wing-beat frequencies of the mutants with that of the wild strain, it is important to estimate as accurately as possible what fraction of any observed differences was due to chance and to external fluctuations and what fraction can be attributed to genetic factors.

As previously described, environmental fluctuations were minimized by flying the animals under rigorously controlled conditions. Nevertheless, due to intangible factors, a certain amount of variability would be expected. The extent of this residual variability was always small, however. As indicated in Tables 1, 2 and 3 the standard errors of the measurements averaged 0.067 thousand wing-beats per minute for the 34 types of animals studied; the average coefficient of variability was 2.87 per cent. Hence it was possible to differentiate the various strains on the basis of even minor differences in their respective frequencies of wing-beat.

Twenty-six specimens of the wild control strain had an average wing-beat frequency of 10.36 ± 0.06 thousand double beats per minute. The reliability of this value has been checked in numerous experiments performed at frequent intervals during the course of the study. It seems justifiable to conclude that if any of the mutant stocks has a wing-beat frequency of less than 10.18 or more than 10.54 thousand double-beats per minute, then a significant effect on its flight has been found.

MUTATIONS RESULTING IN THE LOSS OF FLIGHT

The following mutants showed complete or extensive loss of flight ability:

Vestigial. The area of the vestigial wings is obviously insufficient to support the animal in the air. Furthermore, wing-motion of this mutant has not been observed. As Harnly (1941) has pointed out, this locus determines the flight capacity of the individual not only through its effects upon the wing form, but also through effects upon the neuro-muscular mechanism, a conclusion with which we concur.

Aristapedia. This mutation results in the loss of the aristae and in striking modifications of the antennae, the segments of which resemble those of legs. Flight and wing-motion are absent, although the wings appear to be unmodified. The failure to produce wing movements can not be directly attributed to the absence of the aristae, since the independent mutant, aristaless, is not flightless.

Bithorax. The degree to which this character reaches expression varies widely even after prolonged backcrossing to the wild strain. When severely expressed, flight ability is lost. However, individuals sometimes move the wings at high frequencies when partially anesthetized. In normal flies the halteres are vibrated at the same frequency as the wings, but in opposite phase: the enormous halteres of this mutant usually remain motionless if the animal can be induced to fly. Two different alleles of bithorax were studied, bx and bx^{34e}; the results were similar for both stocks.

Curved. There seems to be phenotypic variation in the curvature of the wings of this mutant. Otherwise the morphology of the wing appears to be normal. Rare individuals will produce wing movement and support themselves in the air for short distances; usually, however, no wing motions occur and, even in the most favorable cases, the motion is ''fluttery'' and stroke-amplitude very reduced.

Taxi. The wings of this mutant are apparently normal except for defects in the flexor mechanism that result in the wings being held in the uplifted, open position. No wing-motion has been observed.

Curly. These flies can occasionally be induced to move the wings rapidly, but fail to give any consistent stroke and are unable to support themselves in the air.

Lyra. This mutant is wholly flightless. Morphologically, ''scallops'' are lost from the two borders of the wing, an effect that is bilaterally symmetrical. The wings are of at least normal length (2.71 ± 0.016 mm), and appear to be unmodified in most respects. The missing scallops reduce the wing-area to 1.64 ± 0.020 sq. mm. from the normal area of about 2.18 sq. mm. One would not, *a priori*, expect this reduction in wing-area wholly to prevent wing-motion. The wings of the mutant, miniature, have an area of but one square millimeter, yet their motion is unimpaired.

Eyeless and cubitus interruptus. About one in twenty of these animals can be induced to fly and support themselves in the air. No animal was found that gave a completely normal stroke and in those cases where wing-beat frequency could be measured it was lower than that of the wild strain. The two individuals on which complete series of determinations were obtained averaged 9.82 thousand double beats per minute, the lowest frequency found for any of the melanogaster stocks.

In summary, it is clear that numerous mutations whose effects are ordinarily considered to be specific structural changes also produce, or are associated with, marked impairment of the flight ability. Furthermore, the mechanisms of this effect are obscure and frequently have no clear connection with the morphological change by which the mutation is catalogued.

MUTATIONS NOT RESULTING IN THE LOSS OF FLIGHT

The remaining twenty-five mutants showed less extensive changes in flight ability than those described above. The wing-beat frequencies of ten of these mutant strains are recorded in Table 1. As previously described, we may expect insignificant variation in wing-beat frequency to fall within the limits 10.18 to 10.54. In Table 1 it is therefore apparent that the mutants, miniature, cut, glass and cinnabar are characterized by significant increase in wing-beat frequency, whereas lobe (homozygous), crossveinless (homozygous) and scute show significant decrease. Sepia and bar fall within the "normal" limits of variation.

TABLE 1

WING-BEAT FREQUENCIES WITH THEIR STANDARD ERRORS, GENERATIONS OF BACKCROSSING TO THE WILD TYPE, AND THE SIGNIFICANCE OF THE DEVIATIONS FROM THE WILD "CONTROL" STRAIN

Strain	No. of flies flown	Generations of backcrossing	Wing-beat frequency (1,000 per min.)	Significance
Wild strain (122d generation)	26	..	10.36 ± 0.06	..
Miniature	16	23	12.26 ± 0.11	+
Cut	11	19	10.88 ± 0.04	+
Glass	15	25	10.87 ± 0.11	+
Cinnabar	23	20	10.77 ± 0.08	+
Sepia	25	27	10.33 ± 0.06	−
Bar				
(homozygous)	21	28	10.33 ± 0.08	−
(heterozygous)	22	28	10.44 ± 0.05	−
Lobe				
(homozygous)	21	29	10.11 ± 0.10	+
(heterozygous)	21	29	10.48 ± 0.06	−
Crossveinless				
(homozygous)	24	21	10.15 ± 0.06	+
(heterozygous)	19	21	10.40 ± 0.06	−
Aristaless	13	31	10.18 ± 0.10	−
Scute[1]	20	27	10.14 ± 0.06	+

The existence of the series of white alleles allowed us to test a single locus more intimately. It is well known that the white locus mutates to varying degrees in terms *of eye pigmentation to give alleles ranging from blood to* white. The question naturally arises as to whether the effects of the white locus on flight parallel these gradations of effects on pigmentation.

The results obtained from eleven alleles at the white locus are recorded in Table 2. Significant effects on wing-beat frequency were found for blood, eosin, cherry, honey, buff, tinged, pearl and white (Reed), whereas apricot, white (Dunn) and white (Williams) are without effect. In this table the alleles are arranged in a graded series in terms of pigmentation. It is clear that the degree to which flight was affected is independent of the effects on pigmentation. Apparently some of the alleles at the white locus have effects on flight and other alleles at this locus do not.

TABLE 2

ALLELES AT THE WHITE LOCUS.
WING-BEAT FREQUENCIES WITH THEIR STANDARD ERRORS, GENERATIONS OF BACKCROSSING TO THE WILD TYPE, AND THE SIGNIFICANCE OF THE DEVIATIONS FROM THE WILD "CONTROL" STRAIN. THE ALLELES ARE ARRANGED IN ORDER OF INTENSITY OF PIGMENTATION

Allele	No. of flies flown	Generations of back-crossing	Wing-beat frequency (1,000 per min.)	Significance
Wild strain (122d generation)	26	..	10.36 ± 0.06	..
Blood	21	18	10.77 ± 0.06	+
Eosin	19	25	10.58 ± 0.05	+
Cherry				
(homozygous)	25	24	10.66 ± 0.06	+
(heterozygous)	16	24	10.32 ± 0.06	–
Apricot	33	23	10.40 ± 0.05	–
Honey	21	20	10.56 ± 0.08	+
Buff	21	11	10.87 ± 0.07	+
Tinged	30	24	10.65 ± 0.07	+
Pearl	21	25	10.83 ± 0.06	+
White				
(obtained from Dunn)	23	25	10.45 ± 0.06	–
(obtained from Williams)	19	30	10.42 ± 0.08	–
(obtained from Reed)	21	27	10.79 ± 0.07	+

X-RAY ISOGENIC STRAINS

Four mutants were studied that had been established by the x-ray method. These consisted of three strains of white and one of apricot. Both homozygotes and heterozygotes were tested in each case. As shown in Table 3 the wing-beat frequencies of none of these strains differed significantly from that of the wild strain or from that of their respective heterozygotes.

The absence of significant effects in this series confirms the results obtained in the backcrossed strains where apricot as well as two of the three strains of white proved to be without effects on flight. If the backcrossed strains had differed from the wild strain by a large number of genes, such an agreement would not have been anticipated.

TABLE 3

WING-BEAT FREQUENCIES WITH THEIR STANDARD ERRORS AND THE SIGNIFICANCE OF THE DEVIATION FOR FOUR ISOGENIC STRAINS ESTABLISHED BY THE X-RAY METHOD

Strain	No. of flies flown	Wing-beat frequency (1,000 per min.)	Significance
Wild strain .... (122d generation)	26	10.36 ± 0.06	....
Apricot			
(homozygous)	17	10.32 ± 0.08	Negative
(heterozygous)	18	10.19 ± 0.07	"
1st White			
(homozygous)	16	10.26 ± 0.08	"
(heterozygous)	21	10.20 ± 0.05	"
2d White			
(homozygous)	27	10.39 ± 0.04	"
(heterozygous)	28	10.31 ± 0.05	"
3d White			
(homozygous)	27	10.58 ± 0.06	"
(heterozygous)	24	10.43 ± 0.06	"

DISCUSSION

The data recorded above reveal that of the 33 homozygous mutant strains studied, 24 per cent. showed complete or extensive loss of flight and 45 per cent. showed significant alterations of wing-beat frequency. In less than a third of the strains was flight unaffected. Of the ten strains in the latter category, seven were at the white locus and five of these were the mutant white itself. Thus the latter appears to be singularly free from effects on flight. In terms of wing-beat frequency these five white strains appear to be identical and perhaps should be grouped together.

There can be little doubt that the observed differences have a genetic basis. Assigning the effect in each case to a particular mutant gene is not justifiable, however, since the number of residual foreign genes and the extent to which they may have participated is unknown. But a consideration of the total evidence strongly suggests that some mutations by themselves have effects on flight whereas other mutations are without effect.

In the case of the eight strains in which flight was wholly or extensively lost, the effects of these mutant genes appear to be so extensive that the degree of isogenism is probably of minor importance. From a standpoint of the survival of these strains in nature, it is therefore apparent that the loss of flight is of vastly greater significance than the comparatively minor morphological changes usually assigned to these genes.

The present data consequently support the theory of manifold gene effects and illustrate the danger of evolutionary considerations based solely on morphological characters.

SUMMARY

By means of a stroboscopic method of measuring the frequency of wing-beat, thirty-three approximately isogenic mutant strains of *Drosophila melanogaster* were tested for physiological differences, as indicated in the flight response.

Twenty-four per cent. of the mutant strains showed complete or extensive loss of flight. The mechanisms of this effect are obscure and frequently had no clear connection with the morphological changes usually assigned to these genes.

Forty-five per cent. of the mutant strains could fly, but possessed wing-beat frequencies significantly different from that of the wild, "control" strain.

In less than a third of the mutant strains was flight unaffected.

The genetical basis of these effects is discussed and it is concluded that in at least a number of strains the effect may be assigned to the mutant genes. Conversely the absence of effects was demonstrated for a number of other mutants.

The present data therefore support the theory of manifold gene effects and emphasize the danger of evolutionary considerations based solely on morphological characters.

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GENETICS OF BODY SIZE AND RELATED CHARACTERS

II. SATELLITE CHARACTERS ASSOCIATED WITH BODY SIZE IN MICE

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PART I described the formation from one stock by selection of (1) a small-bodied race and (2) a large-bodied race of the common mouse. Though attention during the selections was directed solely to changing body-size itself, yet the races so produced have come to differ markedly in several other respects, for which we did not select them. The two races have thus become progressively, and often strikingly, differentiated in the frequency with which they exhibit certain hair-color and ear-length genes; in their activity and behavior; in the comparative length of their various appendages (the tail, hind foot and ears, especially); and in litter size (number of young born per litter).

Being wholly incidental to the body size selections in their first appearance and their subsequent development, these changes are to be regarded as secondary or satellite characters, clustering around and correlated with growth in body size as the primary or central character.

In this paper the differences between the races will be briefly described, the nature of the correlating mechanisms analyzed in a preliminary way, certain basic physiological problems pointed out, and a few applications of more general significance made.

A. BEHAVIOR DIFFERENCES BETWEEN THE RACES

Individuals of the small race of mice are very active and aggressive, and rather savage, as compared with the tamer and more docile large race. The small mice are so agile and elusive that their capture from a cage becomes something of a problem, and they have to be weighed in a container. Their "wildness" is obvious to all who work with them, but no attempt has yet been made to measure or analyze it or to determine its underlying causes. The behavior differences accompanying body size differences may simply be an expression of basic metabolic levels; the large mice do tend to become sluggish and obese.

Domestication is, of course, frequently associated with some increase in both body and litter sizes. In general, the behavior of the mice as they were made larger by selection often recalls the findings of Keeler on the changes of temperament occurring in the breeding of the Wistar rat, and on particular coat colors as "marks of domestication." Fichter and Davis mention further cases of such an association in mammals. It is noteworthy that the changes of temperament are tied up with various colors, which are not necessarily homologous even in rats and mice.

B. Coat Color Differences in the Small and Large Races

It is a matter of some interest, with definite bearing on the nature of size inheritance, that selections made for body size alone, ignoring color entirely, have quite unintentionally altered hair colors in the two divergent races.

The contrasting color types under discussion were all noted in early generations of both S and L stocks, but mice of the small race became preponderantly, and in the end exclusively, intense black, black-and-tan or agouti; they are quite frequently piebald, but apparently never dilute or albino. In them the genes *B* and *D*, and possibly *C*, approach or have actually reached fixation, and *s* persists. In the large race, however, the mice have become solid or self-brown or cinnamon (with an occasional albino), and are often dilute. These facts indicate that the recessive genes *b*, and perhaps *d*, are, or are being, made homozygous, and the piebald factor *s* lost.

Such results had not in fact been anticipated, but can be logically explained along lines of recent genetic research. (1) Various investigators, especially Castle, have reported that genes *b* and *d* characteristically accelerate growth in the mouse, as one of their pleiotropic effects, while *B, D* and *s* (as well as short ear, *se*) retard growth in some degree and make for smaller body size. Selection for larger body size would thus naturally increase frequency of qualitative genes like *b, d* and *S,* while the small race would gradually accumulate and fix the contrasting allels. (2) Since the short ear factor, *se,* is closely linked with dilute, it is not surprising that homozygous short-eared mice, smaller by several grams than their litter mates, still segregate from some pairings of the large race. The pull of *d* in one direction (toward size increase) is greater than that of *se* in the other (size decrease); the cross-over combinations *dSe* or *Dse* will be favored by selection. (3) The occurrence of albinos in the large, but not in the small race, is doubtless the result of chance loss of the *c* allel due to drift in a small breeding population (Wright).

As far as the general divergence in size is concerned, it is easy to emphasize unduly the growth-accelerating or retarding effects of a few qualitative factors. We have handled litters, and undoubtedly could establish stocks, of very large body size which carry all the growth-retarding genes mentioned in (1) above. Selection to increase size would certainly succeed without these particular pleiotropic effects, or in spite of them. This important fact is practically ignored in some recent discussions of size inheritance.

C. CHANGES IN RELATIVE LENGTH OF THE APPENDAGES ACCOMPANYING THE SELECTIONS FOR BODY SIZE

The large and small races are to a merely casual inspection normally well proportioned, and measurements of the cranial, axial and appendicular parts have changed somewhat as one would expect considering the changes in body size. Typical linear measurements have increased in the large and decreased in the small race in the course of the selections to alter body weights. Body length (snout to anus by Sumner's method) of males, for instance, averaged 81.28 mm in S_8 and 96.73 in L_8, a highly significant difference of over 28 standard errors. The lengths of appendages (ears, hind feet and tails) also diverged significantly (Table 1).

This is not to say, however, that all organs and regions of the body have changed at precisely the same rate as the body as a whole. The head itself, and all the various appendages, are comparatively small in the large race. Owing to slower relative growth, the appendages do not keep pace with growth of the body. Table 1 presents relevant data.

TABLE 1

Comparison of Averages of Absolute Measurements (by Sumner's Method), and Relative Lengths of Appendages (Tail, Ear, Hind Foot) in Males of the Small and Large Races of Mice Produced by Eight Generations of Selection for Body Size (60-day Weight) Alone. These Appendages are All Comparatively Shorter in the Large Race, Which in These Respects Resembles Geographic Races Inhabiting Cold Climates

	Small race (S_8)	Large race (L_8)	Difference / standard errors
Absolute length (mm) of:			
body (BL)	81.28 ± 0.44	96.73 ± 0.31	28.6
tail (TL)	75.78 ± 0.58	85.54 ± 0.46	13.2
ear (EL)	12.60 ± 0.07	13.82 ± 0.05	15.2
foot (FL)	17.12 ± 0.10	19.05 ± 0.06	16.1
Relative length of appendage:			
TL/BL	0.931 ± 0.005	0.882 ± 0.005	7.0
EL/BL	0.159 ± 0.001	0.149 ± 0.001	7.1
FL/BL	0.211 ± 0.001	0.197 ± 0.001	10.0

Nature of the correlating mechanism. The remarks we have to make about body and appendage lengths require some short summary of our observations on growth and relative growth (Huxley) in these animals. It is generally appreciated that a fetal mouse is exceedingly short-tailed. At birth the tail is proportionately longer, but is still only about two fifths as long as the body. For a brief period after birth the tail continues to lengthen much faster than does the body itself; this is the period of marked positive heterogony (tachy-heterauxesis) in tail growth. The result is that by the time the mouse body measures 2½ to 3 inches, the tail has become nearly as long as the body. If the mouse body continues to grow even more, however, to 4 or 5 inches, for instance, the tail growth is found to lag behind by negative heterogony (brady-heterauxesis), so that eventually the tail is again found to be definitely shorter than the body. What has been said about the tail applies also to the foot and ear, except that the timing of growth is somewhat different in the latter organs.

The differences in appendage length in the mouse races can now be understood and explained as a case of allomorphism arising out of ontogenetic heterauxesis (Huxley, Needham and Lerner). The growth rate of the small race is generally retarded; its size increase slows down sharply in the second month, and practically ceases at a body length of at most 85 or 90 mm. At this body size the tail and other appendages are still comparatively long. In view of the relative growth described it may be predicted that further reductions of body weight and length in the small race will result in further increases in relative length of the appendages. Ultimately, however, decreases would again be expected.

Growth in the large race, by contrast, is generally accelerated and possibly more prolonged. The body grows on to a length of 110 or 120 mm. The tail meanwhile fails to keep up with the rate of body growth, and the indices, TL/BL, etc., accordingly fall to lower values than in the small race. These indices are all significantly lower (Table 1).

Measurements of body and appendages taken on large-race mice at frequent intervals from birth onward show that relative lengths of appendages match those in the small race at corresponding body sizes, but that when body size exceeds that of the small race the appendages pass farther into the phase of brady-heterauxesis and are relatively shortened. An immature 20-day large-race mouse resembles quite closely a 60-day mouse of the small race in size, body proportions and comparative length of appendages.

The present case, discussed at greater length elsewhere (MacArthur and Chiasson), is possibly the first in which size races of recent and known origin have been available to study allometric phenomena both as ontogenetic processes (heterauxesis) and as phylogenetic divergences attained (allomorphism). From their mode of origin by selection, the two races are likely to differ only, or predominantly, in general size or growth-rate factors, and not (except as chance fixation or drift enters in) in growth factors which act regionally or locally, and might specifically control tail, ear or foot lengths. The differences noted in the comparative size of appendages are thus to be attributed with some certainty to general, rather than to any specific local factors.

D. Changes in Litter Size Accompanying Selection for Body Size

We gradually came to realize, with the progress of the selections for body size, that the number of young born in a litter was rising in the large race and falling in the small race. This difference soon became both striking and significant, as the data in Tables 2 and 3 will show.

In mice, as in mammals generally, there is an age factor in liter size (see Hammond; MacArthur, 1942). In both the mouse races the second or third litters contain, on the average, more young than either the first, fourth, or fifth litters.

The important interracial difference is that the small race had litters of from 3 to 8, the large race of from 3 to 15, young, the range and variability being much greater in the L stock.

Some additional data relating litter size to weight of new-born young and weight of mother are given in Table 4. As compared with those of the small race, young from litters of the large race were more numerous by 84 per cent. and individually heavier by 24 per cent. The col-

TABLE 2

BODY SIZES (60-DAY WEIGHTS IN GRAMS) AND LITTER SIZES (YOUNG BORN PER LITTER) IN SMALL AND LARGE RACES OF MICE PRODUCED BY EIGHT GENERATIONS OF MINUS AND PLUS SELECTION, RESPECTIVELY

	Small race (S_8)	Large race (L_8)	Difference / standard error
Body weight (grams)			
Males	16.14 ± 0.25	33.71 ± 0.31	44.1
Females	13.80 ± 0.19	28.43 ± 0.39	33.7
Number of young per litter			
First litter	5.00 ± 0.19	9.22 ± 0.70	5.8
Second litter	6.05 ± 0.32	10.75 ± 0.78	5.6

lective weight of a whole litter in the large race was over twice as much as in the small. Reproduction was equally "expensive" in the two races, if we judge from the fact that in both, the total litter weight is about a third that of the mother just after the birth of the young. But the weight of an individual progeny comprises only 3.6 per cent. of the mother's weight in the large race, and about 6.7 per cent. in the small. Delivery of the young is probably an easier process for the large race mother.

TABLE 3

FREQUENCY OF OCCURRENCE OF LITTERS OF 3 TO 15 YOUNG IN THE SMALL (S_8) AND LARGE (L_8) RACES OF MICE

Small race													
first litter	3	5	12	5	3								
second littler	1	3	5	4	3	6							
third litter			3	1	3								
Large race													
first litter	1		1	1	2	4	1	1	1	3	2	1	
second litter		2			1	1	2	2	3	2		1	
							9	10	11	12	13	14	15

The physiological correlation of body size and litter

TABLE 4

NUMBER OF YOUNG AND SIZE OF BIRTH-FED YOUNG IN SUCCESSIVE LITTERS OF THE SMALL (S_8) AND LARGE (L_8) RACES OF MICE, AND THEIR RELATION TO MOTHER'S BODY SIZE AFTER BIRTH OF YOUNG (ALL WEIGHTS IN GRAMS)

	Mean litter size	Mean wt. of birth-fed young	Total wt. of litter	Mother's weight	Litter wt. / mother's wt.
Small race					
first litter	5.0	1.15	5.66	17.06	.33
second litter	6.1	1.22	7.12	19.65	.36
third litter	6.0	1.13	7.10	20.14	.35
Large race					
first litter	9.2	1.49	13.67	41.05	.33
second litter	10.1	1.47	14.92	46.77	.32

size. The facts of this association are clear enough. Why, then, does a small race female have few young, and a large race mother about twice as many in a litter?

Litter size in mammals may be limited and controlled in general by: (a) the number of ova made available by the female, (b) the proportion of these eggs successfully fertilized by the male and (c) the prenatal mortality of zygotes between fertilization and birth of the young. These factors seem to be important in the order named in causing the difference in litter size in the mice. It is hardly tenable as a hypothesis that litter size is primarily equal in both races, but is cut down in the small race by extra mortality to suit the capacity of the small mother. Direct examination of pregnant females and counts (mainly by Mr. L. P. Chiasson) of their corpora lutea and fetuses, show that the two races differ greatly only in number of ova released. Corpora lutea averaged about 7.5 in small, and 13.6 in large race females (of generation 11). The ceiling on egg number, like that on fetuses, or young born, is nearly twice as high in the large race.

On purely anatomical grounds, it might be thought that a large mouse, with proportionately large ovaries, would, of course, liberate ova in numbers corresponding to the mass of her ovarian tissue. In mammals at least the known facts are against this simple explanation, for as many eggs appear to be freed from one ovary, or a half ovary, as from two. Reviews by Hammond, and by Moore, cover this and other phases of the problem of mammalian fertility.

From the general physiological and clinical evidence, the correlation between body size and litter size depends on endocrinal links, such as the growth and gonadotropic hormones of the anterior pituitary, which presumably mediate in some way between the size genes and their diverse ultimate effects. The precise nature of the nexus remains to be determined. Size genes may control primarily the size of the pituitary, and thence, secondarily, both body size (by the growth hormone) and litter size (by the follicle-stimulating gonadotropic principle). More likely the size genes primarily regulate general body growth, and thence, by laws of relative growth, the size of the pituitary, whose gonadotropic hormone, acting quantitatively, determines the litter size. The number of ova released by a female thus in all probability depends, not upon the size or even the maturity of the ovaries, but on the amount, concentration, activity of the F.S. substance, which either from injections or pituitary transplants easily induces (see, *e.g.*, Rowlands) marked hypertrophy of ovaries and increased output of eggs (superovulation).

In any event, the mouse data suggest that general body size factors exert a remote and indirect control over litter size. There is little reason to think that the two races carry different "litter size genes" or "fertility factors" as such.

DISCUSSION

It is, perhaps, only to be expected, after all, that selections to alter body size should result in coordinated changes in some other quantitative and qualitative characters. Only on the view that there is a single specific gene "for" each character could one expect otherwise. More nearly justified is the contrary view that a gene typically helps determine, and controls grades of expression of, a whole system or syndrome of supposedly unrelated characters and parts.

The characters thus grouped proved to include all kinds: continuous and discontinuous; morphological, physiological and psychological; qualitative (as hair colors), meristic (as number of young) and quantitative (body size, activity, etc.). The correlating mechanisms involved are doubtless equally various, some being causal in nature and permanent in effects (as in the cases of pleiotropic, or physiological correlations) and others merely statistical and temporary (as in case of linkage, *e.g.*, of short ear in the large race of mice). Correlations due to linkage or to "drift" are likely to be sporadic and erratic; those due to manifold gene effects are likely to be of more regular and widespread occurrence, and susceptible of formulation as more general "rules," like the association of large body size with large litters in races of many species of mammals (MacArthur).

If a gene acts pleiotropically its several effects are not clearly separable. In achieving its diverse end results ontogenetically, a variety of mechanisms and processes, cyto-histological, physiological, endocrinal and nervous, are frequently concerned. Selection for a faster growth rate must provide more cell units in the body as a whole and in its several parts, including the endocrinal glands. This offers a basis for gradations of functional activity in hormones, and these in turn for changes, often more or less regional and local, in physiologically correlated characters. Changes in body size are bound to introduce changes in the relation of body surface to mass, and in metabolic levels and activity. By heterogonic growth they also alter relative length of appendages and perhaps even number of young born in a litter. Such varied correlated characters trace back link by link by one causal chain or another to more general, antecedent growth processes and ultimately to common genes or gene complexes.

Factors controlling a character like body size are undoubtedly numerous enough to be represented in many or all chromosomes and segments of chromosomes. Size genes are quite sure to be in some degree genetically linked with qualitative, multiple, balancing or modifying factors controlling other characters. In this sense all quantitative characters are associated by linkage, as Anderson has shown for several graded characters in a tobacco species cross. Variability in several respects and characters, both quantitative and qualitative, is thus set free simultaneously by new combinations following crossing over. The characters in such a complex are held together, at least briefly, and are changed concurrently by selection directed on any one of them.

Modern genetic theory thus returns, after a long diversion, to the general principle so insistently emphasized by Darwin, that selection produces correlated, rather than a series of independent, changes. Some of the correlated changes described in the mice are obviously adaptive when associated. It is only fitting, for instance, that a large mouse should bear the large litters. But, by way of warning against putting too much trust in pure a priori reasoning about the fitness of things, we should note that the number of nipples for feeding the extra young is not increased in the large race; nipple number is apparently an independent character in mice, as in sheep. Nor is the length of the gestation period noticeably changed by the selections for growth rate.

A group of correlated characters, adaptive enough frequently to become established in nature by natural selection, is seen in the size races of species of warm-blooded animals of wide range and more or less continuous distribution. The geographic races inhabiting colder habitats (high latitudes and altitudes) tend to be those of larger body size (Bergman's rule), and those presenting relatively smaller body surface and smaller appendages (Allen's rule); in both respects they economize on heat lost by radiation. That large-bodied races should also have larger litters (the "litter rule" for mammals) or clutches (Rensch's "clutch rule" for birds) may also be considered adaptive. In any case the characters enumerated in these climate rules are clearly related as a common complex, based directly or indirectly on the same general size factors, arising together in development, and often keeping together in their geographic distribution.

In the course of further raciation and speciation such complexes of associated characters are often worked over and extensively reorganized. Between allied species of mice of the genus *Peromyscus* Clark has found that differences in "body size and proportions cannot be attributed primarily to general size factors and heterogonic growth," the variations in tail, body and foot lengths, for instance, being in this case "due primarily to special size factors, genetic and developmental."

APPLICATIONS

It should be of some interest to field naturalists and museum biologists making faunal surveys that so many "climate rules" or trends, originally formulated and established as quite independent of each other (see Rensch), prove to have a common underlying basis.

It is rather remarkable that two races of mice, bred from one foundation stock by only three years of artificial selection and maintained throughout in a common environment, should resemble so closely in several respects the geographic races of many mammalian species found in nature occupying opposite ends of a temperature cline (lowland vs. alpine; or Southern vs. Northern races in Europe and North America).

The positive association disclosed between body size and litter size is of such wide-spread occurrence in mammals that it is possible to generalize with the broad rule (MacArthur) that, within a species of mammals, litter size tends (with some exceptions) to average greatest in larger races of laboratory animals, in larger breeds of domestic animals, and in the larger geographic races of wide-ranging wild mammals (or birds) in nature.

We have given reasons for thinking that the same rule holds also for man, since the largest-statured human races certainly tend to produce large litters (that is, fraternal twins, triplets, etc.) most frequently. The incidence of fraternal twin births is three or four times higher among North Europeans, or West African (American) Negroes than among small races like the Japanese.

From the practical agricultural point of view, the qualities most prized in high-producing live stock are interrelated. Thus large body size, faster growth, more economical gains from feed and rapid and efficient reproduction are all intimately associated, and selection becomes an especially powerful tool for the breeder seeking a simultaneous improvement in these useful characteristics.

SUMMARY

Small and large races of mice produced from one stock by eight generations of selection for body size alone, came to differ strikingly and significantly, not only in body size, but unexpectedly in many other characters and traits as well (behavior, hair colors, relative length of the appendages and litter size). The large race, for instance, has certain distinguishing coat colors (brown, dilute, etc.); is more docile and inactive; has comparatively shorter ears, feet and tail; and bears many more young in a litter.

The coat colors are such as are controlled by genes, either known to exert pleiotropic growth-accelerating effects, or probably fixed by chance drift. Behavior differences may be associated with metabolic levels. Appendages are proportionately small because they grow less rapidly than the body in the last stages of growth. Large litters are due to superovulation in the large race, evidently regulated by the gonadotropic hormone of the anterior pituitary.

Litter size and length of appendages appear to be dependent, like satellites, upon body size as the central and dominating member of a complex of correlated characters, with a common developmental basis in growth. Differences between the mouse races in litter size or length of appendages are determined, not by special fertility factors or ear-length genes, etc., but, in great part at least, by the same common and general multiple size or growth rate factors that control body size.

Several applications to general biological problems are suggested.

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THE CORRELATION BETWEEN ANTIGENIC COMPOSITION AND GEOGRAPHIC RANGE IN THE OLD OR NEW WORLD OF SOME SPECIES OF COLUMBA[1]

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INTRODUCTION

VARIABILITY of biological forms associated with geographical location has come to be a subject of primary and increasing importance in biology. Studies on this subject have been made largely on races or subspecies of an organism, although there are many which are concerned with diversity of species according to habitats. Several excellent reviews have recently been written on this subject and to these the reader is referred for discussions of the various findings and for references to the literature. Among such reviews are those by Dobzhansky (1941), Huxley (1942), Mayr (1942) and Timofeeff-Ressovsky (1940).

During investigations of the interrelationships of the cellular antigens of 11 species of the genus Columba, it was noted that there was a tendency for the species to fall into one or the other of two groups. Furthermore, the native habitat of the members of one of these two groups was in the Eastern and of the other in the Western Hemisphere. The analysis of the data on the association of these antigenic characters with habitat in the two hemispheres is given in this paper. Naturally, any statements which are made in this paper are applicable only to the species which have been tested.

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[3] The authors are indebted to Professors L. J. Cole and R. A. Brink for reading this manuscript and for their comments on it.

Various reports from this laboratory have shown that the cellular antigens, which distinguish the blood cells of one species from those of another, segregate in the backcross offspring as would be expected if these characters are genetically determined (Irwin and Cole 1936, 1940; Irwin, *et al.* 1936; Irwin 1939). These and all studies by other workers on cellular antigens in other species make reasonable the conclusion that all the antigens of the blood cells in the various species tested—and probably those in all species—are gene-determined.

If this conclusion be true, it follows that the interrelationships of the cellular antigens of related species would be in effect an analysis of these various species in terms of the genes which have biochemical effects. The relationships of the cellular antigens of human cells to those of the higher apes and monkeys are discussed by Wiener (1943). The geographical distribution of the antigens (commonly called "blood groups") $\overline{A}$, $\overline{B}$, $\overline{AB}$ and $\overline{O}$ of humans is also discussed by this author. For a more detailed account of this latter subject, see Boyd (1939).

A recent paper (Irwin and Cumley, 1943) has analyzed most of the gross relationships of the cellular components of eleven species of Columba. This analysis has shown, among other things, that each of these species appears to be a biochemical entity in comparison with any other species, but has interlocking relationships of antigenic characters, and therefore of their causative genes, among all the other species. It is now proposed to examine the data of the above report for a possible correlation of the antigens of the species with their geographical locations. In so far as is known, the antigenic characters of the blood cells are not influenced by the environment and therefore represent more or less constant genic effects wherever they appear.

The details of the technique used in obtaining the agglutination reactions are described in the preceding paper (*loc. cit.*). Briefly, an antiserum to a particular species of Columba was absorbed by the cells of another species and the resulting "reagent" was tested with the cells of all available species of the genus. This procedure was carried out with the antiserum to each of the different species, using in respective absorptions the cells of the other species.

The interpretation of the agglutination tests with the various reagents may be explained by an example. The antiserum to *flavirostris* cells was absorbed by those of *guinea*. This reagent agglutinated the cells of seven of the nine species with which it was tested, and from these results it can be stated that the cells of the species giving agglutination with this reagent did so by virtue of one or more antigens which each shared with *flavirostris* to the exclusion of *guinea*. And since this reagent did not agglutinate the absorbing cells (*guinea*) nor those of *palumbus*, one can deduce that *guinea* shares with *flavirostris* most if not all the antigens that this latter species shares also with *palumbus*.

Presumably, the closer the biochemical relationship between any two species, the greater will be the proportion of antigens which are *common* to them; and the proportion of these characters *specific* to either species will be correspondingly less. As the relationship between species decreases the relative proportion of *common* antigens also will decrease, and that of *species-specific* antigens will increase. The phrase "genes with effects on antigens of the blood cells" may be substituted for "antigens" in the preceding sentences.

It may be assumed that the present geographic distribution of the species of pigeons is correlated, in some measure, with the phylogenetic relationships of the species. With this in mind, the various species were arranged in terms of their geographic distributions in the hemispheres, as given by Peters (1937). The areas occupied by these several species are given in Fig. 1. The species of the New World used in these tests are *Columba fasciata, flavirostris, leucocephala, maculosa, picazuro* and *rufina*. Those of the Old World are *Columba guinea,*

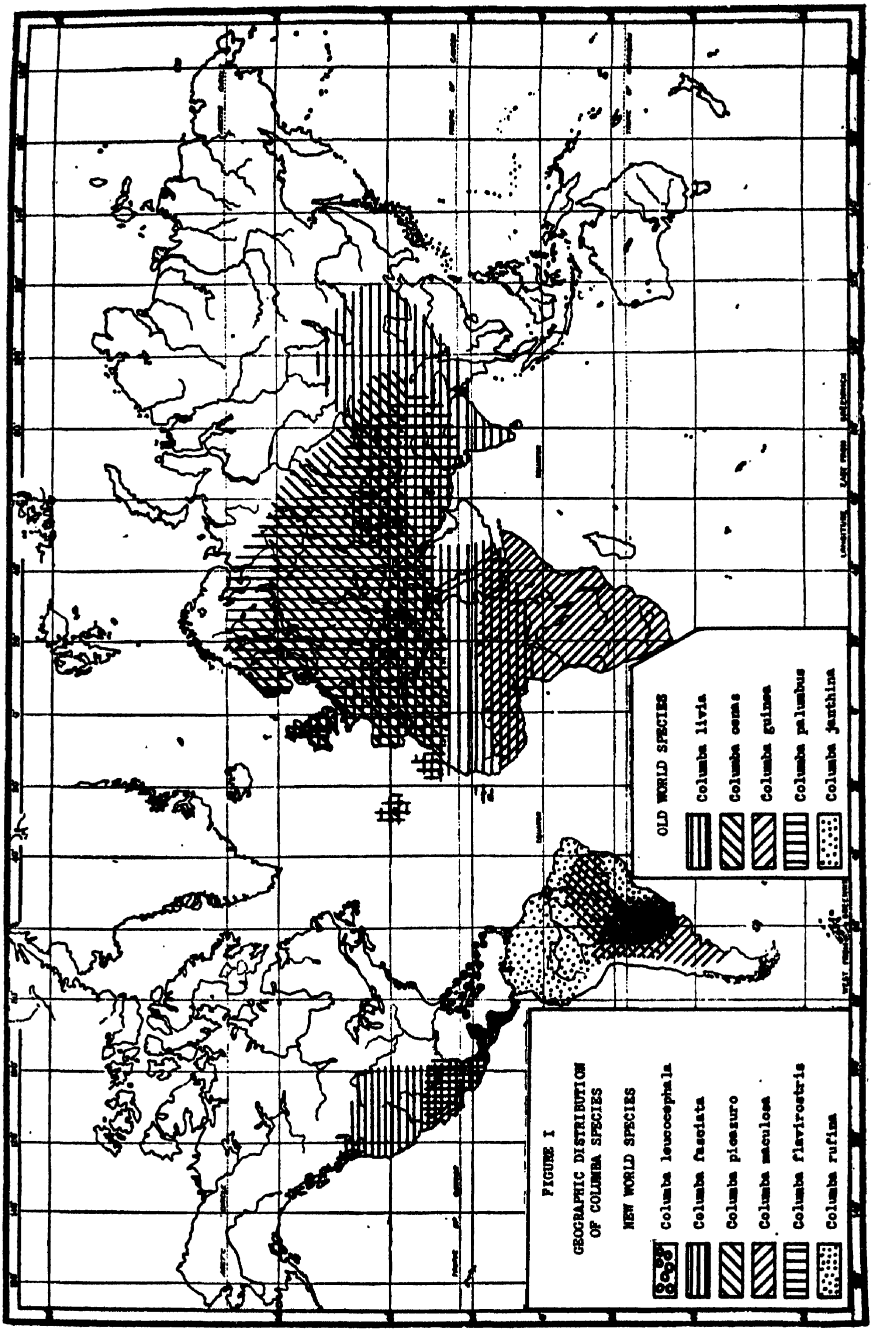
FIGURE I
GEOGRAPHIC DISTRIBUTION OF COLUMBA SPECIES
NEW WORLD SPECIES
Columba leucocephala
Columba fasciata
Columba picazuro
Columba maculosa
Columba flavirostris
Columba rufina
OLD WORLD SPECIES
Columba livia
Columba oenas
Columba guinea
Columba palumbus
Columba janthina

FIG. 1.

janthina, livia domestica, oenas and *palumbus.* None of the species native to the Old World has been found wild in the New World, and vice versa. (As is well known, the domestic pigeon of this continent, *C. livia domestica,* is an imported descendant of the *C. livia* which is native to Europe, Asia and northern Africa.)

TABLE I

A SUMMARY OF THE AGGLUTINATION REACTIONS OF REAGENTS, PREPARED FROM ANTISERUMS TO SPECIES OF COLUMBA, WITH THE CELLS OF ALL THESE SPECIES, GROUPED ACCORDING TO HABITAT IN THE OLD OR NEW WORLD, RESPECTIVELY

A. A composite of the reactions of antiserums to species of the Old World after absorption by the cells of :

		Old World species						New World species						
Cells used in tests	Cellular reactions	ea	iina	ia	nas	lumbus	tals	ata	ostr	leuc cepl	mac llosa	pica	rufi	Tot
Old World species	+	10	8	16	9	6	49	21	21	10	19	21	21	113
	0	1	0	0	1	1	3	0	0	0	0	0	0	0
New World species	+	15	12	24	16	7	74	15	22	0	19	8	5	67
	0	2	0	0	2	10	14	3	0	8	0	3	13	27

B. A composite of the reactions of antiserums to species of the New World after absorption by the cells of :

		Old World species					New World species					
				n	lum	tal	scia	avir	acul			
Old World species	+	14	24	9	4	51	13	20	20	11	11	75
	0	3	0	0	0	3	4	0	0	1	6	11
New World species	+	29	36	30	14	109	20	20	20	13	8	81
	0	0	0	0	0	0	0	0	0	0	12	12

The digits represent the number of species of either the Old or New World, listed according to the reaction of their cells, either positive ("+") or negative ("0"), with the various reagents. See text for more complete explanation.

It will be noted in Fig. 1 that there is considerable overlapping in both continents of the areas inhabited by certain of the species. In the Eastern Hemisphere, for example, the ranges of *livia, oenas* and *palumbus* coincide in parts of Asia, southern Europe and northern Africa, and of *livia* and *guinea* in central Africa. So also do the ranges of *maculosa, picazuruo* and *rufina* overlap in South America, and of *fasciata, flavirostris* and *rufina* in Central America.

The data given in the table of the previous article (Irwin and Cumley, 1943) were summarized in two main groups, depending upon whether the antiserums were developed against Columba species of the Old or New World. Thus, in part A of Table I in the present paper, the various antiserums to the Old World species are grouped together, and the reactions following the absorptions by the cells of the respective species are listed, giving the number of both positive and negative reactions with cells of those inhabiting the Old and New World, respectively. Similarly, in part B of the table there is given the same kind of composite reactions of antiserums to New World pigeons with cells of species of both the Old and the New World. It is admitted that this division of reactions into the two classes (according to presence of absence of agglutination) does not give a complete picture of antigenic relationships, but it will serve as a starting point in the analysis of possible differences in the species according to habitat. Furthermore, it is conceivable that reagents prepared from other antiserums than the several to each species which were used in these tests might not always give the same reactions, or lack of them, as are summarized in the table. However, it is unlikely that the general picture of interrelationships among these species would be materially changed even if many more antiserums were employed in parallel tests. This statement can be made with reasonable assurance, for the application of the principle of reciprocal agreement of reactions, as explained in the previous paper, showed that the discrepancies were relatively few.

Old World Antiserums

The reaction of all antiserums, with the cells of the species of the Old and New World, against the several species of the Old World (*guinea, janthina, livia, oenas* and *palumbus*) are combined in part A of Table I according to whether the absorptions were made by the cells of *guinea, janthina* or of one of the three other species. The results of the absorption of an antiserum by the homologous cells, as of anti-*guinea* serum by *guinea* cells, are not included in the summary. Nor are the reactions of an antiserum to the absorbing cells given as these, being usually negative, would tend to confuse the relationships. All questionable reactions in the original table are eliminated from this summary, as are those which were discrepancies according to the criteria explained in that paper. Thus, in part A of Table I, the antiserums against species of the Old World (*janthina, livia, oenas* and *palumbus*), when absorbed by the cells of *guinea,* gave agglutination of cells of Old World species in 10 combinations and no reaction in one. With cells of New World species, there were 15 positive reactions and two negative. If each antiserum to Old World species had been absorbed by the cells of all the other Old World species, there would be 16 combinations possible with cells of species of the Old World, other than the absorbing cells, and 24 with those of the New World. It will be noted in the table that the total number of possible reactions was but seldom observed, either because of discrepant reactions, involving only a small fraction of the total, or the lack of cells of a species at the time of testing. This latter condition was particularly true for the cells of *janthina, palumbus* and *leucocephala.*

The antiserums against the Old World species, when absorbed with cells of species of the Old World, were tested in a total of 52 combinations with cells of these species, resulting in 49 positive and three negative reactions. These same reagents were reactive in 74 combinations of cells of New World species and produced no agglutination in 14 such combinations. It is interesting that the absorptions by the cells of *palumbus* were responsible for 10 of these 14 negative reactions. That is, the cells of *palumbus* possessed many of the cellular antigens that were shared by other species of the Old World with certain New World species. The differences in the number of positive and negative reactions of these reagents with cells of the Old and New World species, respectively, suggest that there is a definite tendency for at least certain of the cells of Old World pigeons to share all the antigens among themselves that are shared with these species of the New World. Indeed, the species of the Old World probably share *more* antigens among themselves than are shared with pigeons of the New World.

Much greater differences in reactivity of cells of the Old and New World species occurred following absorptions, by the cells of New World species, of antiserums to Old World pigeons. Agglutination was observed in each of 113 combinations of such reagents with cells of birds of the Old World as compared to 67 positive reactions and 27 negative reactions in 94 combinations with cells of New World species. These differences are highly significant. One of the most pertinent findings of this analysis of the data is that no species of the New World removed all the antibodies for cells of Old World species from antiserums against the Old World species. That is, none of these New World pigeons shared as many antigens with any species of the Old World as were shared *among* the species of the Old World.

On the other hand, each New World species except *flavirostris* and *maculosa* removed antibodies, for cells of other species than itself among those of the New World, from certain antiserums to species of the Old World. For example, there were 13 negative reactions among cells of the New World following absorptions by *rufina* cells of these antiserums to Old World species. Referring to the table with the complete data in the previous paper (*loc. cit.*), it may be seen that two New World species, *fasciata* and *rufina,* either removed antibodies for the cells of other New World species entirely from the antiserums to the Old World pigeons, or left antibodies capable of reacting with them only slightly, if one may trust the degree of reaction to be a reasonable criterion. Unfortunately, only two of these antiserums (anti-*guinea* and anti-*livia*) were absorbed with *leucocephala* cells, but the reactions of these two reagents, combined with those following absorptions by the corpuscles of *fasciata* and *rufina*, suggest strongly that *fasciata, leucocephala* and *rufina* are very similar in content of cellular antigens shared with Old World pigeons. The cells of *picazuro* appear to contain a smaller quantity of these antigens, and those of *flavirostris* and *maculosa* a still smaller amount.

If the *common* substances represent more or less stable genic effects in the evolution of each of these species, it might be argued that *fasciata, rufina* and probably *leucocephala* have changed from the ancestral stock slightly less in these genes than did *picazuro*, and much less than did *flavirostris* and *maculosa*. Naturally, if these several New World species evolved from other than a common stock, more divergence would be expected than if but one ancestral origin had obtained. But the evidence strongly indicates that, although *flavirostris* and *maculosa* have different parts of the antigens of Old World pigeons which are *shared* by these six of the New World, the other species (*fasciata, leucocephala, picazuro* and *rufina*) possess all or nearly all of the combination of such antigens of these two species, plus others in addition. From this point of view the evidence points definitely toward a common ancestry of these six species of the New World.

However, in addition to the varying amounts of antigens shared with the Old World species and among themselves, each of these species has antigens which distinguish it from each of the other species tested. It is the variation in the amounts of cellular antigens shared with other species and the possession of specific antigens which distinguish it from any other single species that make each species a biochemical entity. Naturally, other biochemical characters, such as those of the serum, also will contribute to this end.

New World

A parallel summary of the reactions to antiserums of Columba species of the New World is given in part B of the table. Representatives of *janthina* and *leucocephala* were but seldom available for their cells to be used in the absorptions of these antiserums, although absorptions of *leucocephala* antiserum were made and the reactions to the reagents so produced are included.

It may be seen from these results that, following absorption of antiserums to New World species by the cells of four of the five Old World species, there were 51 positive reactions with cells of pigeons of the Old World and three combinations with no agglutination. The lack of reactions in these three combinations is a partial reflection of the close relationship of the cellular antigens between *guinea* and *palumbus,* as stated in the preceding paper (*loc. cit.*), since the cells of *guinea* by absorption removed antibodies from two antiserums for those of *palumbus.* Tests of these reagents on the cells of New World pigeons gave positive reactions in each of 109 combinations. That is, no pigeon of the Old World shared either the same or more antigens with any species of the New World than were shared with another of the New World. These particular results are in entire agreement with those of the reciprocal tests; i.e., reactions of antiserums to Old World species with the cells of these species, following absorptions by cells of New World pigeons.

But when cells of New World pigeons were used in absorption of the antiserums to species of this group, there were 75 positive and 11 negative reactions with cells of birds of the Old World, and 81 positive and 12 negative reactions with those of species of the New World. All the negative reactions of the latter group were obtained with reagents produced by absorptions with the cells of *rufina,* whereas either *fasciata* or *rufina* cells, and in one instance those of *picazuro,* removed antibodies for corpuscles of Old World species.

GENERAL CONSIDERATIONS

On the basis of the presence or absence of agglutinations of the cells of the various species of the Old and New World, it is clear that absorption of antiserums to pigeons of the Old World by cells of those of the New World did not completely remove the antibodies for any Old World species. A complementary situation was found in summarizing the reactivities of antiserums to New World pigeons in that absorptions by the cells of birds of the Old World did not remove all the antibodies for any of these species of the New World. It appears reasonable to conclude from these results that there are some antigens in these species of the Old and New World, respectively, that are not shared by any single species of the other hemisphere. (The possibility is not excluded, however, that such antigens might not be shared by a combination of two or more species from the other hemisphere. Data which test this possibility will be presented in another paper.) These relationships may be summarized as follows:

1. There are cellular antigens shared more or less uniformly by both Old and New World species of Columba.
2. Within the species of the Old and New World, respectively, there appear to be some antigens which are shared primarily within each group, but in varying proportions.

Thus, it appears that there are classes of antigens which are *common* either to all these species of Columba (category 1), or within the species of the Old or New World (category 2) in varying interlocking arrangements. In addition, each species definitely possesses antigens which distinguish it from every other single species. These might be described as being (3) antigens of species of either the Old or New World, portions of which are contained in many and perhaps in all species of the respective groups. A diagrammatic representation of these categories has already been given (Irwin and Cumley, 1940).

Some additional evidence on the relationship proposed above is provided if to the criterion of the presence or absence of agglutination is added that of the degree of reaction, or probable quantity of agglutination. Comparisons based on the degree of reaction are not as accurate indices of relationships as the presence or absence of a reaction, but should not be ignored in this analysis, particularly the questionable reactions (labeled "?" in the table in the preceding paper). The most plausible explanation of the questionable reactions is that the relationships, if any, dependent upon such reactions are likely to be slight. If these be added to the totals given in Table I, the results are as follows: For Old World antiserums absorbed by cells of species of the Old World, there were 6 questionable reactions of these reagents in tests with Old World cells, 6 with New World cells; if absorbed by cells of New World pigeons, there were no questionable reactions in tests with Old World cells, but 11 with New World cells. In the composite of antiserums to New World pigeons, following absorptions with cells of Old World species, there were 5 doubtful reactions in combinations with Old World cells, and none with those of the New World. If exhaustions were made by cells of New World species, there were 3 such reactions with Old World cells and one with those of the New World. None of these questionable reactions detracts from the argument of the division of these species into two groups according to habitat. Whatever deductions may be made from them would conform to those already proposed.

What appear to be the most obvious inconsistencies in the original table are the reactions of the reagents of anti-*livia* serum absorbed, respectively, by the cells of *janthina* and *leucocephala*. The agglutinations of Old World cells with this *leucocephala* reagent are of less degree than they are with the other, and thereby do not entirely conform to the postulate of group differences between Old and New World species. Whether this same kind of exception would have been found with other Old

World antisera cannot be predicted. The only other antiserum which was absorbed by the cells of these two species was that to *guinea,* and these reagents did not produce exceptional results in tests with the various cells.

Within these five species of the Old World group *guinea* and *palumbus* are the two whose antigens are most closely related, according to reasons given in detail in the previous article (*loc. cit.*). The other three species (*janthina, livia* and *oenas*) appear to be related to each other and to *guinea* and *palumbus* in varying degrees, depending upon the species with which the comparison is made. For example, the cells of *oenas* removed most of the antibodies from anti-*fasciata* and anti-*flavirostris* serums for the cells of both *guinea* and *livia,* showing that *oenas* shared with these two species most of the cellular antigens shared by them with *guinea* and *livia.* Leaving out the details of these complex relationships, it seems that these species of the Old World tend to resemble each other somewhat more than any one of them tends to resemble a single species of the New World. On the other hand, particularly in the antigenic complex which each species of the New World shares in varying amounts with those of the Old World, there is, as previously stated, evidence which very definitely suggests a common ancestry of these six species of the New World.

The results of the tests of antigenic relationships among these 11 species suggest strongly that, from the point of view of cellular antigens, these species of the Old and New World fall into two groups according to habitat in one or the other of the hemispheres. (A comparable grouping was proposed by Cumley and Cole (1942), using as a criterion the various color patterns, and including many more species than have been tested for antigenic relationships.) The species within each hemisphere have been shown by these tests to be definite biological entities, but still they are more alike *within* than *between* the groups. Within the species of the New World, *picazuro* and *rufina* are very closely related biochemically, as are *guinea* and *palumbus* in those of the Old World.

For reasons given in the previous paper (Irwin and Cumley, 1943), it is probable that the erythrocytes of *guinea* differ from those of *palumbus* by the products of one or more genes on each of three or four chromosomes. Although the actual number of chromosomes in these species of Columba is not known at present, the best estimate is that each has about the same number as was observed by Painter and Cole (1943) in *livia* and ring-dove (*Streptopelia risoria*), *viz.*, about 30 pairs. Genes on chromosomes of *guinea,* with antigenic effects, other than those on the three or four which distinguish *guinea* from *palumbus,* will then produce antigens *common* to these two species. These probably represent the effects of one or more genes on many, if not on all, of the chromosomes other than these three or four. At the moment there exist no criteria for estimating the number of cellular characters by which *palumbus* differs from *guinea,* or by which *picazuro* and *rufina* differ one from the other. It seems reasonable, however, to assume by analogy with the small number that distinguish *guinea* from *livia,* that there are relatively few involved in these other cases.

If the basic premise be admitted that these species of Columba have evolved from a common stock—and any other premise would be difficult indeed to maintain in the light of the data on the biochemical characters—one can postulate certain events that almost certainly have taken place in the evolution from the ancestral stock to the present species. For reasons already given in this paper, it appears justifiable to state that the species of the New World have evolved from a common ancestral stock. To account for the two main lines of divergence into species of the Old and New World, respectively, it may be assumed that there was a separation of forms within the common ancestral stock, and from one of these arose the species of the New World. But whether only two forms, or potential forms, existed at the time of this separation can be only a guess.

One can account most simply for the fact that in two closely related species, as *guinea* and *palumbus,* the majority of the genes which effect cellular characters now produce antigens which make the species alike, by alternate proposals or by a combination of these. Thus, disregarding the possibilities of position effect, either (a) the genes for cellular characters in these two species have changed very little in their evolution from the ancestral stock, or (b) whatever changes took place were for the most part parallel. To use a concrete illustration, we can cite the experimental findings which show that *guinea* differs biochemically from *livia* in the effects of one or more genes on each of five or six chromosomes (Irwin *et al.*, 1936), giving rise to antigens $\overline{\mathrm{A}}$, $\overline{\mathrm{B}}$, $\overline{\mathrm{CD}}$, $\overline{\mathrm{E}}$ and $\overline{\mathrm{F}}$. Also, from unpublished data it appears that *palumbus* shares with *guinea* all of two ($\overline{\mathrm{A}}$ and $\overline{\mathrm{F}}$), parts of at least two more of these antigens ($\overline{\mathrm{CD}}$ and E and possibly $\overline{\mathrm{B}}$) which distinguish *guinea* from *livia,* as well as all or practically all the cellular components which are shared by *guinea* and *livia.* (It is possible to make the latter statement, since *palumbus* cells removed all or nearly all the antibodies from *guinea* antiserum for the erythrocytes of *livia,* as shown in line 26 of the table in the previous paper.)

If, then, *guinea, livia* and *palumbus* trace back to a common ancestral stock, it follows that, during their separation into distinct species, gene changes occurred in five or six chromosomes of either *guinea* or *livia.* Whether these changes from the ancestral form occurred primarily in *guinea,* or only in *livia,* or some in both cannot be answered definitely. As the changes from the ancestral stock occurred in *guinea,* in *livia,* or in both, to give the demonstrable genic effects ($\overline{\mathrm{A}}$, $\overline{\mathrm{B}}$, $\overline{\mathrm{CD}}$, $\overline{\mathrm{E}}$ and $\overline{\mathrm{F}}$) which now set *guinea* apart from *livia, guinea* and *palumbus* pursued a parallel course in respect to certain antigens specific to *guinea* in relation to *livia; viz.,* $\overline{A}$, $\overline{F}$ and parts of the $\overline{\mathrm{CD}}$ complex and $\overline{\mathrm{E}}$, and perhaps of $\overline{\mathrm{B}}$. Both species, however, underwent sufficient change in genic material to make each a biological entity with cellular characters peculiar to itself.

The interactions given in the table of the preceding article (*loc. cit.*) show further that *guinea* shares with *oenas* some antigens not found in *livia* (lines 23 and 67 of the table in the preceding article). Likewise, *guinea* and *livia* have in common cellular components not present in *oenas* (lines 25 and 53), and *guinea* shares with *palumbus* all or practically all the antigens which it shares with both *oenas* and *livia* (line 26). Furthermore, *guinea* has some cellular characters in common with *janthina* to the exclusion of either *livia* or *oenas* (lines 23 and 25), but shares with *palumbus* all or nearly all the substances which it (*guinea*) possesses jointly with *janthina* or *livia*, and possibly with *oenas* (line 26). From these relationships of cellular antigens the deduction seems justifiable that *guinea* pursued one evolutionary path in comparison with *livia*, a slightly different one with *oenas*, another with *janthina*, but that *palumbus* accompanied *guinea* all or almost all the way on each of these three routes.

In relation to the species of the New World, *guinea* shares substances with each of the six of this group to the exclusion of either *janthina* or *livia* (see lines 21 and 23 in the table of the preceding article), and shares with *fasciata, leucocephala, maculosa, rufina* and perhaps with *picazuro* but not with *flavirostris* some substances *not* held in common with *oenas* (line 25 of the table). Furthermore, as stated earlier in this paper, *fasciata, leucocephala, rufina* and probably *picazuro* contain the same, or most of the same, antigens that are shared with Old World pigeons in general and with *guinea* in particular, while *flavirostris* and *maculosa* have a lesser quantity of the common substances than do the other four species. To return to a consideration of the various evolutionary paths which *guinea* travelled in relation to the several species of the New World, one may state that *guinea* took only slightly different roads in relation to *flavirostris* and *maculosa*, respectively, and that the other four species of the New World—*fasciata, leucocephala, picazuro* and *rufina*—accompanied *guinea* on these routes and to a more or less common point beyond. Again referring to the known genetic characters ($\overline{A}$, $\overline{B}$, $\overline{CD}$, $\overline{E}$ and $\overline{F}$) by which *guinea* differs from *livia,* it has been found that all or parts of $\overline{A}$, $\overline{CD}$ and $\overline{F}$ are shared by *guinea* with most of the New World species. The occurrence of these or closely related cellular substances ($\overline{A}$, $\overline{CD}$ and $\overline{F}$) in various species of both Old and New World makes it appear that these particular genetic characters are those which have persisted throughout their evolutionary course in these several species whereas the changes from these have taken place in *livia.* Such genic effects along with those *common* to *guinea,* or other species of the Old World, and the New World pigeons would probably be those of greatest age in the several species. Otherwise one would need to hypothesize parallel mutations to explain their occurrence in these various species. It seems highly probable that the genes which produce substances *common* to any two species are more numerous than those producing the antigens *specific* to either species, so the possibility of parallel mutations accounting for the block of cellular components *common* to both Old and New World species seems rather remote.

The principal steps in the evolutionary paths of each of the other species of the Old World could be traced in the same manner as described for *guinea,* with the expectation that for each species a particular pattern with respect to the others would be found. And since comparaable interrelationships exist within the various species of pigeons of the New World, from them may be deduced an outline of the evolutionary pattern for each species of this group. However, such deductions will be more exact if further tests are made of these antigenic relationships, particularly the extent to which a species may share antigens with another to the exclusion of two others, as will be shown elsewhere. (It is particularly unfortunate that the cells of *janthina* were not always available for testing. Occupying as it does a more or less isolated habitat off the eastern coast of Asia, the interrelationships possible with the other species might have shown whether this species represents a bridge between Old and New World forms, as might be suspected if the pigeon species spread from the Old World to the New via eastern Asia.)

What appears to have taken place in the evolution of these species in the different hemispheres is probably a large scale model of how the evolution of other species may proceed within a smaller geographic range. But for these species of Columba there does not appear to be a correlation between closeness of antigenic relationship and present habitat *within* the hemispheres. As stated above, the species of the Old World which are most closely related antigenically are *guinea* and *palumbus*. Their ranges do not overlap, according to present information, yet each coincides in range with at least one other species of a less degree of this kind of biochemical relationship. Similarly, in the New World, although *picazuro* and *rufina* are the two most closely related, *rufina* shares geographic range with *maculosa* almost to the same extent as with *picazuro*. Nearness of habitat, then, need not necessarily be an index of degree of relationship of species, at least not of biochemical relationship.

SUMMARY

An analysis of the data on antigenic interrelationships of the blood cells among eleven species of the genus Columba indicates that these species tend to fall into two groups. The species comprising one of these groups lives in the Old World, those of the other in the New. The reasons for this grouping are based primarily upon the data which are interpreted as indicating that the antigens of each species of either the Old or New World are more like those of any other species of that hemisphere than they are like those of any single species of the other. All available evidence points to the conclusion that the cellular antigens of a species are many, and are gene-determined. On this basis, it appears that a separation took place in the ancestral stock early in the evolutionary his-

tory, and that the species of the New World evolved from one of the forms, those of the Old World from another.

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THE DISTRIBUTION OF THE OSMIINE BEES OF THE DESERTS OF NORTH AMERICA

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IN the course of revisional studies of various genera of Osmiinae a repetition of certain distributional patterns was observed in all genera characteristic of the North American desert regions. It is the purpose of this paper to present the data involved, which is derived from a study of nearly four thousand specimens from the arid regions of the southwestern United States, and to suggest possible reasons for the peculiarities of distribution noted.

The Osmiinae are solitary bees which nest in the soil, in wood or, more rarely, in snail shells, unused portions of mud wasp nests, etc. As with all bees, they are entirely dependent upon flowers for food. Many of the species of the subfamily are confined in their pollen collecting to a few, usually related, species of flowers and are called oligolectic. Such species usually have but a single brood each year, the winter being passed in the prepupal state and emergence of the adults taking place at the season when certain favorable flowers are in bloom. After a few weeks of activity, new nests are provisioned, eggs laid in them, and the adults die. Species with longer seasons of flight, often with two or even more broods each year in some areas, commonly collect pollen from many unrelated species of plants. These bees are termed polylectic.

The bees of the desert areas may be arbitrarily divided into two overlapping groups based upon their season of flight and the nature of the plants upon which they feed. The first of these groups consists of genera which, in the desert, fly primarily in the spring and are dependent upon the flowers of herbaceous mesophytes which grow up and bloom during the short period when the desert is relatively moist. The bees of this group are primarily Holarctic types, such as *Andrena, Dufourea* and *Tetralonia.* The second group consists of genera which visit the flowers of the characteristic xerophytes, such as *Larrea, Prosopis* and *Cercidium,* not only in the spring but also later in the year. This second group includes forms whose nearest relatives are Neotropical (such as *Centris, Ericrocis, Protoxaea* and apparently *Perdita*), as well as representatives of such widespread genera as *Halictus* and *Megachile.* There is scarcely a genus of bees every species of which may be unquestionably placed in one or the other of these groups; nevertheless, the division is quite evident. The Osmiinae adapted to the deserts fall for the most part in the second group, although they, like the characteristic elements of the first group, are derivatives of Holarctic genera. This northern origin of the Osmiinae is evident from their distribution. They are found in the Holarctic and Ethiopian faunal regions; no species of the subfamily is known from South America or Australia.

It appears probable that the group of genera here considered (Tribe Osmiini[1] ofMichener, 1941, *Am. Midl. Nat.,* 26: 147–167) arose in the Palearctic region, because it is there that the species of some of the widely distributed and morphologically apparently primitive genera are most numerous and diversified, and it is there also that the lines of separation among these genera become evanescent. Indeed some genera are so closely related that it seems certain that they must have arisen from ancestors which would fit our definition of extant genera. Thus it is probable that the characteristics which delimit *Hoplitis* were in existence in the ancestral stock at the time when *Anthocopa* was differentiated.

Since the characters used in determining the phylogenetic relationships of the genera and a phylogenetic tree for them have been presented in a previous paper (Michener, 1941), it seems unnecessary to repeat them here.

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[1] It now appears probable that this group of genera is not best regarded as a tribe. However, it constitutes a monophyletic group. Genera of the subfamily Osmiinae outside of this group scarcely invade the edges of the desert areas.

OSMIA, HOPLITIS AND DICERATOSMIA

These are the genera of the Tribe Osmiini which are rare in the deserts, being represented there by relatively few individuals of a small number of species closely related to or identical with species found in adjacent more humid regions. A brief discussion of them is included merely to contrast these forms with those considered below. *Osmia, Hoplitis* and *Diceratosmia* are all Holarctic genera. Both *Osmia* and *Hoplitis* are abundant in species as well as in individuals in the mountains east and west of the desert areas and in the cool mesophytic areas north of them. Their rarity in the desert contrasts strongly with the greater abundance of many genera of aculeate Hymenoptera in the arid regions than elsewhere. *Diceratosmia* in North America is found only east of the Rocky Mountains except for a single species extending into the southwestern deserts.

ANTHOCOPA

The American forms of the genus *Anthocopa* are confined to the area west of the eastern foot of the Rocky Mountains. The five American subgenera are probably derived from two ancestral forms of *Anthocopa* which migrated independently into northwestern America from Asia. The subgenera *Atoposmia* and *Hexosmia* are montane and northern groups, probably similar to these ancestral types. The first is confined in its pollen collecting to *Pentstemon,* the second to Hydrophylaceae. Each of these subgenera, or an ancestral form similar to each, has apparently given rise independently to distinctive desert derivatives. Thus *Eremosmia,* a desert subgenus closely related to *Atoposmia,* contains about six species which are oligolectic on various Hydrophylaceae and Leguminosae. *Phaeosmia,* confined primarily to the desert, is a subgenus of four known species, all of which collect pollen from Compositae. The relationship of this subgenus to *Hexosmia* is comparable to that of *Eremosmia* to *Atoposmia*. *Xerosmia* is a very distinctive desert subgenus, probably derived from a *Hexosmia*-like ancestor. The two species of *Xerosmia* are oligolectic on species of *Cryptantha*, and as in the genus *Proteriades*, which also feeds on this plant, the mouthparts are short and furnished with numerous hooked bristles. I do not believe that this similarity in mouthparts is indicative of a close relationship between *Proteriades* and *Xerosmia*;

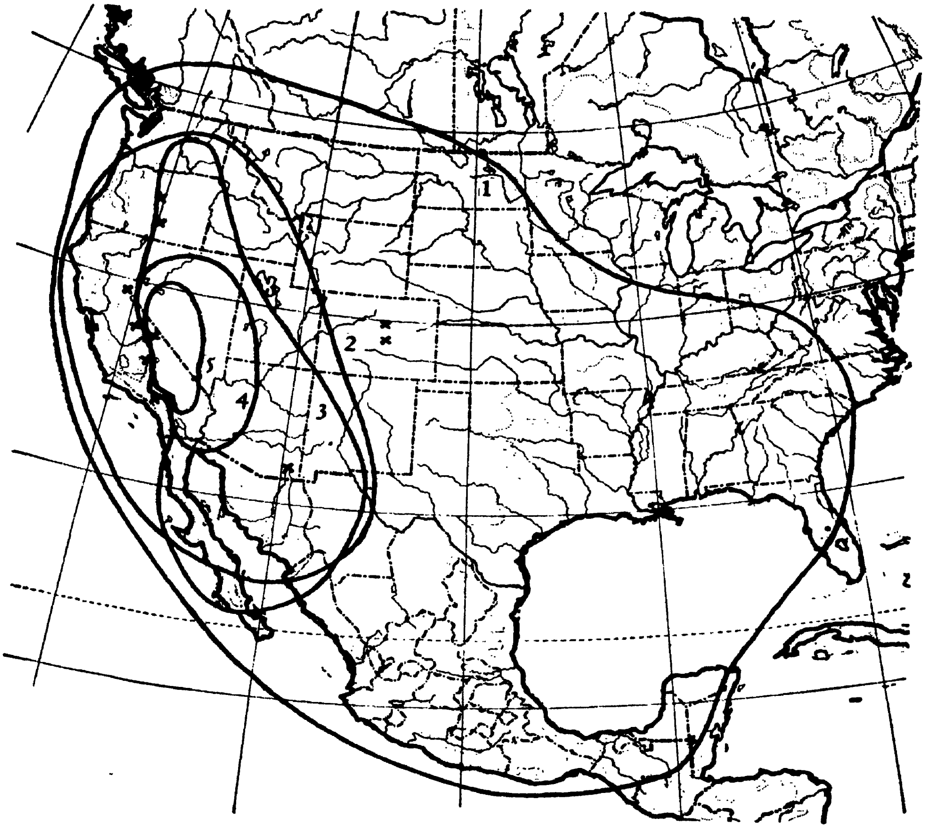

FIG. 1. Map of North America, showing the distribution of the subgenera of *Ashmeadiella*. Line 1 encloses the area occupied by *Ashmeadiella* s. str.; 2, *Arogochila;* 3, *Chilosima;* 4, *Corythochila;* 5, *Cubitognatha*. The known localities for *Titusella* are marked by x. (The cut for this figure is used through the courtesy of the *American Midland Naturalist* and its editor, Dr. T. Just.)

rather it seems likely that the resemblance is a result of convergent development.

The three desert subgenera of *Anthocopa* thus far have not been collected outside of California; indeed, most of the specimens taken have come from locations in the desert within easy view of the mountains which mark the western edges of the desert areas. Thus, although one species of *Phaeosmia* occurs in the coastal part of southern California, all other species belonging to the subgenera characteristic of the desert occur in a narrow zone along the western margins of the Great Basin and Colorado Desert, scarcely larger than that indicated for *Cubitognatha* in Fig. 1.

It is an interesting sidelight that the genera *Megandrena* and *Ancylandrena,* whose relationship to the primarily Holarctic genus *Andrena* is nearly as close as that of *Eremosmia* and *Phaeosmia* to the other subgenera of *Anthocopa,* are restricted to the same small area occupied by *Eremosmia* and *Phaeosmia.*

ASHMEADIELLA

The genus *Ashmeadiella* is widely distributed in North America, ranging from southern Canada to Yucatan and from the Atlantic to the Pacific, but is well represented only in the western part of its range. The close relationship of the species of *Ashmeadiella* and the limited distribution of the genus as a whole is evidence that it is a younger genus than *Anthocopa,* from which it is apparently derived. The wide distribution and morphological diversity of *Anthocopa* suggest relative antiquity. *Ashmeadiella* is divisible into several subgenera. The subgenus *Ashmeadiella* s. str. appears to be the most primitive of the subgenera, being similar morphologically to certain groups of *Anthocopa.* The details of the subgeneric characters and a phylogenetic tree have been omitted in this paper since they were presented previously (Michener, 1939, *Am. Midl. Nat.,* 22: 1–84).

In connection with the theory that the subgenus *Ashmeadiella* s. str. is more primitive than the other subgenera, it is interesting to note that many of its species are polylectic and fly more or less continuously through much of the summer. Thus *A. californica* (Ashmead) has been collected by P. H. Timberlake at Riverside, California, from April 11 to November 1. On the other hand, the majority of the species in the other subgenera are oligolectic and have short seasons of flight, a condition characterizing some species of the subgenus *Ashmeadiella* s. str. as well.

When plotted on a map (Figure 1) the distributions of the various subgenera form a series of concentric areas whose common center is the western part of the Great Basin and western Colorado Desert, in which region species as well as individuals of all of the subgenera (except *Titusella*) are most numerous. While the rare and little-known montane subgenus *Titusella* is properly excluded from this paper on desert bees, its dispersal probably having been hindered rather than facilitated by the desert areas, it is included in the discussion for the sake of completeness. In the following list the subgenera are named in the order of decreasing area occupied with the number in parenthesis after each indicating the number of species and subspecies included: *Ashmeadiella* s. str. (39), *Arogochila* (15), *Titusella* (4), *Chilosima* (2), *Corythochila* (2) and *Cubitognatha* (1).

PROTERIADES

The genus *Proteriades,* unlike the previously mentioned genera, is closely related to the Holarctic genus *Hoplitis* and occurs only in California and, no doubt, certain adjacent states. It consists of probably fifteen or twenty species, all oligolectic on species of *Cryptantha* and having specialized mouthparts probably adapted for use in flowers of this plant.

Although a few species occur in the coastal parts of California, the majority are found in the western Great Basin region and in the Colorado Desert. It is in these desert regions, also, that the greatest morphological diversity is found.

Discussion

It will be seen from the foregoing that at least four groups of Osmiinae have independently adapted themselves to desert conditions in western North America. These groups are (1) *Anthocopa,* subgenus *Eremosmia;* (2) *Anthocopa,* subgenus *Phaeosmia* and probably *Xerosmia;* (3) *Ashmeadiella* and (4) *Proteriades.*

The distributional problems involved are twofold. First, why are the desert groups concentrated in or restricted to the extreme western edge of the desert? Second, why are the distributional areas of the subgenera of *Ashmeadiella* concentric with the western margin of the desert as the center?

Both questions might be answered by assuming that the desert forms are relicts of groups more widely distributed at a time when the desert areas were larger but limited now to a favorable area, some subgenera of *Ashmeadiella* being more restricted than others. Such an explanation is difficult to believe, since we are dealing with genera containing many closely related species and having every appearance of being relatively young. One would also expect some of the relict species to occur in the deserts of Arizona and New Mexico which in most elements of their biota are very similar to those of California; yet it is only the more widespread subgenera of *Ashmeadiella* which are found in those areas.

It is easier to believe that the desert groups originated in the region where now they are most abundant, that is, on the western edge of the desert, and spread thence in varying degrees over the arid regions and even into relatively humid areas. It is then necessary to determine why parallel desert groups should not have arisen elsewhere, for example in New Mexico where the Rocky Mountains meet the desert areas.

A possible explanation of the absence of desert groups of Osmiinae in other areas is that, guided by the north and south mountain ranges and climatic zonation, the so-called ancestral genera, after entering North America from Asia, migrated rapidly southward along the Pacific coast far into California before they were able to spread eastward into the interior states. The Osmiine genus *Chelostoma,* found in America only in our Pacific states, is an example of a genus still exhibiting such a distribution. A genus so distributed would first come in contact with arid regions in the particular area where the desert groups apparently center. There, in a region of very steep topographic and climatic gradients, it would perhaps give rise to desert derivatives such as the groups under consideration. Eastward and subsequent southward spread of the ancestral genera along the Rocky Mountains might have taken place much later than the southward dispersal along the Pacific coast, so that contact with desert conditions in the southern Rocky Mountain region may have taken place so recently that no distinctive desert groups have developed there. Such a theory requires that the desert groups be not older than Miocene, since the desert itself is of that age. It may be that *Ashmeadiella* arose in this way considerably earlier than the others, so that certain species have had time to readapt themselves to moderately moist climates and have spread over much of North America.

While it seems probable because of the similarity in distribution that the various desert groups of Osmiinae arose in the same manner, it may, nevertheless, be true that one of the foregoing hypotheses would apply best to certain groups, while the other might explain the origin of others.

Assuming, then, that the desert genera and subgenera originated where they now occur, let us return to the distribution of *Ashmeadiella.* The facts presented above suggest that from a center of origin in the western Great Basin and western Colorado Desert, the various subgenera, with the probable exception of the montane *Titusella,* arose and radiated as a series of waves over the continent. The one which produced species having the greatest collective tolerance to environmental conditions (the most primitive and presumably the oldest) adapted itself to habitats covering the greatest territory, whereas the most highly specialized, perhaps the youngest, is narrowly restricted. Yet each remains in the entire territory which it populated, not being replaced by succeeding waves. If this is a correct explanation, it is indeed remarkable. Why should not some of the subgenera appear at and radiate from other points? Perhaps *Titusella* is an example of a group which did arise at a point other than the center of origin of *Ashmeadiella.* A possible explanation for the apparent common center of origin of the various subgenera may involve the climatic extremes and intense solar radiation of the region, factors possibly responsible in part for extensive speciation there. It is, moreover, a region of many isolated mountain ranges with adjacent diverse habitats which would perhaps favor selection of biotypes and perhaps eventual geographic isolation of new forms. Furthermore, in the apparently favorable environment of the western parts of our desert areas there has been the largest number of individuals and hence the greater chance for mutations and possibly for the development of new types which might eventually become additional species and even subgenera.

Since the powers of dispersal of bees appear to be great, it seems very improbable that the restricted ranges of the various species and subgenera should be entirely due to lack of time necessary for further migration. It is likely that a species will rapidly occupy the entire area environmentally suited to it and not separated from it by impassable barriers. Changes in climate or topography or in the tolerance of the species for environmental factors would then be necessary in order further to enlarge the range. Therefore, factors other than the length of time required for dispersal are probably responsible for the limited distribution of certain species and subgenera. The extent of the dispersal probably depends more on the rate of production (or the time available for the production) of new biotypes adapted to new environmental conditions than on the time available for dispersal.

The migrations of the subgenera must have taken place since the last major climatic changes in the area concerned; otherwise the clear-cut distributional pattern of concentric areas would have been disturbed. To a large extent the region now occupied by *Ashmeadiella* was not greatly affected by Pleistocene glaciation, and the dispersal of *Ashmeadiella* could have continued with little interruption through this period. If the hypotheses presented are correct, they may lend some confirmation to parts of the much criticized "Age and Area" theory of Willis.[2] Possibly such distributional effects can be recognized only in those groups which have spread rapidly in areas in which climatic and topographic changes have been slight during the time of dispersal.

SUMMARY

With the exception of four groups, the American Osmiinae are northern and montane forms, rare in the deserts and virtually absent in the neotropics. These four groups, independently derived from northern forms, are characteristic of a zone in which they probably arose along the western margin of the desert of central and southern California. Three of the groups are largely confined to this zone. The fourth, *Ashmeadiella,* has a broader range, covering most of North America, but is divisible into several subgenera, the distribution of which form concentric areas (Fig. 1) whose common center is in the region referred to above. Individuals and species of the more widely distributed subgenera are most abundant in this area. The morphologically generalized subgenus is the widespread, largely polylectic one containing many species, while the more restricted subgenera consist of fewer species, which are for the most part oligolectic. This distributional pattern suggests the possibility that from a common center of origin in the western Great Basin and Colorado Desert, the subgenera arose and radiated.

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[2] J. C. Willis, "Age and Area," x + 259 pp., Cambridge Univ. Press.

REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

IN this section reviews and notices are given of current publications on general biology and of specialized works which have an important bearing in this general field. Emphasis is given to books and major articles which fall within the special scope of THE AMERICAN NATURALIST, in that they deal with the factors of organic evolution.

REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

A Contribution to the Theory of the Living Organism. By W. E. AGAR. Melbourne: Melbourne University Press (in association with Oxford University Press), 1943: 1–207. 12s, 6d.

PHILOSOPHY, psychology and biology are combined in this interpretation of life processes. The ideas, in so far as they diverge from ordinary concepts, rest largely on Whitehead's panpsychism. That philosophy, though so heavily relied upon, is admittedly difficult to understand—a vast understatement.

Perception and appropriate behavior are central themes in Agar's theory: organisms and their parts are "subjects," which perceive stimuli, anticipate consequences and react accordingly. Embryonic development is regarded as a complex of instinctive behaviors. Purpose, striving, feeling and satisfaction are ascribed to the activities of all but the simplest animals and of plants; and are also attributed to the physiological functions of individual cells and of higher "nexus" (tissues and organs). There is a hierarchy of "agents" intermediate between the cells and the "Central Agent," which is the individual animal, integrated chiefly by the nervous system. It is even suggested that what are ordinarily treated as attributes of the human mind are involved in the compounding of chemical substances, molecules and atoms. In the lower organisms and substances the brain is replaced by a "mental pole."

It is repeatedly pointed out, however, that these psychological terms are used without any connotation that the organs, cells and lower organisms feel, perceive, anticipate and react with consciousness. Their "feelings," however, are the evolutionary antecedents of consciousness. The actual functions of all organisms are admittedly physical, but through evolution, purposive function to an increasing degree has become a characteristic of life processes. Life therefore transcends the simple materialism of Loeb.

The restricted connotations which are ascribed to the psychological terms lead the reader to wonder at times whether the differences between Agar's philosophy and current biological thought may not lie largely in the choice of words. He applies to the activities of lower organisms terms that are ordinarily associated with the human mind. Others describe the same acts in physical terms. Differences in interpretation are vastly less fundamental than the respective terminologies would indicate. Nevertheless, there is some real distinction in concepts, at least differences of degree, for Agar projects supposedly human attributes backward into the evolutionary series farther than most biologists would.

Agar applies a teleological view only to the direct attainment of "hormic goals," through specific responses and physiological functions. There can be no striving toward the satisfaction of other than immediate needs. It is claimed to be beyond the realm of science to ascribe purpose to life processes, including those of ontogeny and phylogeny, which lead indirectly and remotely to favorable biological consequences. Apparently it is beyond the mental powers of lower organisms and cells to look that far forward.

The theory of natural selection is held to provide the only plausible explanation for these processes leading to remote consequences. The Lamarckian idea on which other psychobiologists have rested their case is regarded as untenable, because even if acquired characters be accepted as heritable, the Lamarckian factor must be drastically limited. Since on Agar's theory there can be no "striving" toward remote functions Lamarckian inheritance and evolution can not be attributed to the many biological processes which lead indirectly—as in the ontogeny of the eye—to favorable biological consequences.

Plants and Vitamins. By W. H. SCHOPFER. Authorized translation by N. L. NOECKER. Waltham, Mass.: The Chronica Botanica Co.; New York: G. E. Stechert and Co., 1943, i–xiv, 1–393, 3 pls. $4.75.

WITH the tremendous interest in the subject of vitamins exhibited by plant physiologists in recent years this book should be welcomed by them as well as by others interested in the subject, and no one is better equipped to write such a book than the author, who has been a pioneer in this field.

The author has divided his book into three sections. In section one, "Synthesis of Vitamins in Plants, Auxo-autotrophic Plants, Research Methods," he takes up the synthesis and the uses of vitamins by the green plants. After discarding many proposed definitions for vitamins he proposes a definition of his own. A vitamin is "an organic substance, the need for which results from the loss of the capacity for its synthesis, whose action is catalytic (active in small amounts), quantitative, and markedly specific." Section two, "Vitamins in Relation to Plants Unable to Synthesize Them, Growth Factors of Microorganisms," takes up in considerable detail investigations on the nutrition of such organisms as yeasts, lactic acid bacteria, Staphylococcus, etc. Also the function of some vitamins as coenzymes is discussed. Some pages are devoted to vitamins in relation to growth hormones. Section three, "General Problems Involving Vitamins," deals with vitamins in the soil and fertilizers, external factors influencing the vitamin content of food plants, vitamins and sexuality and symbiosis. A chapter is devoted to microrganisms as test objects for vitamins, but the author does not give any details of procedure. In the opinion of the reviewer this should have been done.

The author has made an attempt to correlate and explain some of the plant growth phenomena familiar to the plant physiologist in terms of vitamins, and the reviewer believes he has succeeded to a considerable extent. Again and again the author points out the unsatisfactory state of our knowledge of vitamins and this is bound to act as a stimulus to further research on the part of the reader. A very important function of any book should be to stimulate and encourage further research for the truth, and in this respect Professor Schopfer's book should prove of much value. A criticism should be offered because of an insufficient bibliography. In too many instances he refers to the work of certain authors but no citations are made and the reader will be able to locate the papers referred to only after consulting other authors.

F. G. GUSTAFSON

Studies in the Genetics of Drosophila. III. The Drosophilidae of the Southwest. Directed by J. T. PATTERSON. Univ. Texas Publ., 4313, 1943: 1–327, col. pls. 1–10, pls. 1–15, figs. 1–66, maps 1–16. $2.50.

SYSTEMATICS, life history, morphology, zoogeography, population biology and cytology are all advanced in this contribution, which helps to break down the walls between these cubicals of zoology.

The major portion of the volume is devoted to a systematic analysis of the Drosophilidae of the Southwest, by J. T. PATTERSON. The field explorations were very extensive and the species were thoroughly studied. Many are illustrated on the ten handsome colored plates. Other illustrations portray the male and female reproductive systems, the egg and the puparium, all of which exhibit valuable characters. As a result of the studies by Patterson and others the systematics of the Drosophilidae now rivals that of the Culicidae. The relative abundance of the species in various Southern, Southwestern and Mexican states is tabulated. The total records of identified individuals run into many thousands. For one plot in Texas very extensive data were secured on the seasonal fluctuations in the abundance of the species of *Drosophila.* Temperature is shown to be a factor of prime importance.

The geographical distribution of the species of *Drosophila* is treated by J. T. PATTERSON and R. P. WAGNER. Locality records are spotted on 16 maps, and the ranges are stated. The distributions are analyzed by regions and to some extent by habitat. Widely distributed species are discussed, and the role of introductions is considered. The relative abundance of various species in different populations is tabulated at length. The relationships of the Nearctic forms are held to lie with both the Palearctic and the Neotropical types. Since the Neotropical Realm has been intensively explored for *Drosophila* only in Mexico, it is quite possible that what is here called "Neotropical" may refer to an independent, Middle American biota, rather than to one of South American origin. Middle American types are numerous and diverse in certain groups, such as the fresh-water fishes.

In the last paper of the series LINDA T. WHARTON presents a significant comparative analysis of the metaphase and salivary chromosome morphology in 88 strains of *Drosophila.* One general conclusion is that gross alteration of the metaphase chromosome structure is not always paralleled by an equivalent change in the salivary chromosome. Another point is that wide alterations in the arrangement of the chromosome elements have occurred during the divergence and evolution of the species of *Drosophila.*

Statistical Analysis in Biology. By K. MATHER. New York: Interscience Publishers, Inc., 1943: 1–247, figs. 1–9. $4.50.

"IT IS very rarely that the full value of a biological experiment can be realized before the observations have been subjected to a suitable statistical analysis." On this well-warranted assumption the author presents anew the common methods of statistical analysis. As Snedecor did, he follows Fisher very closely. That he has properly interpreted that master of modern statistics is assured in the Foreword, written by R. A. Fisher himself: "The present work, designed as a more general introduction to statistical methods for biological investigators, shows the same practical grasp of the essentials of good experimentation [as does Mather's previous book, 'The Measurement of Linkage in Heredity'], and the same deliberate avoidance of what is extraneous. It is very simply written. . . ." The last statement is interesting, as a quite different appraisal is often heard expressed toward Fisher's own books.

A second assumption, that "statistics is the mathematics of experiment," may be challenged. Statistics is a tool of research, quite as valuable in observational as in experimental science. It is the mathematics of racial analysis and of economics quite as much as that of experiment. Biologists following the observational methods—for example, human biologists and systematists—may find the treatise by Simpson and Roe more pertinent to their needs. Experimental biologists, however, will have in Mather's new book an excellent statement of current statistical methods.

Mather follows what have now become the established traditions of statistical writers: proposing a new set of symbols, and failing to give any list or index of them. He recommends that "in presenting the results of any test of significance the probability itself should be given," but follows the custom of placing special reliance on certain levels of probability ($P = .01$ and $P = .05$). Tables are now available by which one may obtain precise estimates of P, and it is high time that biologists fully realize that values of P between .05 and 1.00 are of significance, to a degree of reliability that is inversely proportional to the magnitude of the value. There are no levels at which the indication of significance suddenly changes from one of complete reliability to one of moderate acceptability and thence to one of no reliability at all. Evidence needs be weighed to more than two or three degrees.

NOTICES OF NEW BOOKS

An Outline of General Physiology. Second Edition, Revised. By L. V. HEILBRUNN. Philadelphia and London: W. B. Saunders Co., 1943: i–xii, 1–748, figs. 1–135. $6.00.—The prodigious amount of scholarly work which went into the first edition of this treatise has now been supplemented by a thorough digest of recent advances. New sections deal with "the electron microscope; localization of enzymes in cells; colloid chemistry of the nucleus; tracer elements, and carbon dioxide syntheses. The greatest changes are to be found in the completely rewritten chapters on enzymes, vitamins, and protoplasmic oxidation." With two thousand new references it is more than ever a synthesis of the science of general physiology. It is the product of a dynamic investigator, who presents his subjects as a living, growing entity. The author's own researches and theories on such fundamental subjects as protoplasmic viscosity, anesthesia, the colloid chemistry of protoplasm and the physiological roles of calcium are given some degree of preeminence—but would one expect or want it to be otherwise?

The Permeability of Natural Membranes. By HUGH DAVSON AND JAMES FREDERIC DANIELLI. Cambridge: at the University Press; New York: The Macmillan Co., 1943: i–x, 1–361, figs. 1–73. $4.75.—"Organisms could not have evolved without relatively impermeable membranes to surround the cell constituents. This barrier between the inside and the outside, the inner and external world of each living unit, has been and always must be considered one of the fundamental structures of a cell. . . . There can be no doubt of the fundamental importance of cell permeability . . . but no general books on cell permeability have appeared for over ten years. . . . Cell permeability had passed from the qualitative to the quantitative stage and the detailed data now available would baulk less enthusiastic authors, even in normal times. . . . Cell physiology will be grateful indeed for this summing up of a subject which is destined for rapid development under the stimulus of modern methods of exploring molecular dimensions and molecular arrangement. Viewpoints may differ but the facts remain. These are systematically and logically presented in this timely volume."—From the Foreword by E. NEWTON HARVEY.

A Guide to Bird Watching. By JOSEPH J. HICKEY. Oxford University Press, New York, 1943: i–xiv, 1–262, drawings by F. L. Jaques. $3.50.—The contribution of amateurs to ornithological science has been tremendous. By means of this available man power ornithologists have been able to attack and solve problems quite beyond the present reach of investigators in other fields of biology. Nevertheless, there is a wide gap between the results that could be accomplished and those actually being obtained by this great body of bird students. This first American guide to bird study should do much toward directing the work of amateur bird students into useful channels.

The author wisely refers his readers to the work of James Fisher and Margaret Nice for information on the literature of bird watching and the study of bird behavior. His own book effectively treats such subjects as bird migration, population, distribution, banding of birds and methods of bird study. A very useful appendix includes an outline for life history study, a classified bibliography and a very full list of American bird clubs.

Every one interested in birds should have this very stimulating and instructive book.—J. VAN TYNE.

Archivos de Zoologia do Estado de São Paulo. Volume III (Tomo XXVI da Revista do Museu Paulista), 1942: i–vi, 1–849, illustr. **Papéis Avulsos do Departamento de Zoologia,** Secretaria da Agricultura, Indústria e Comércio, Vol. II, 1942: i–iv, 1–336, illustr., and Vol. III, 1943: i–v, 1–336, illustr.—The Brazilian state of São Paulo has long been known as a center of zoological research. These three volumes, recently received, give abundant evidence that natural history continues to be actively prosecuted there. Several North American specialists join hands with their Brazilian colleagues in helping to make known the immense fauna of Brazil. The volume of the Archivos contains two large reviews, one by J. LANE AND N. L. CERQUEIRA on the mosquitoes of the tribe Sabethini and one by CARLOS O. DA CUNHA VIEIRA on the bats of Brazil. HENRY W. FOWLER contributes a bibliographic check list of the coastal fishes of that country. Entomology predominates, but many groups of animals are dealt with in the three volumes.

SHORTER ARTICLES AND DISCUSSION

AN EXPANSION OF JONES'S THEORY FOR THE EXPLANATION OF HETEROSIS

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JONES (1917) developed a theory for the explanation of heterosis which has been accepted by most geneticists and plant breeders. Briefly, this hypothesis is as follows: (1) a large number of genes are responsible for the differentiation of most quantitative characters and (2) those genes favorable to the production of the desirable quantitative character are at least partially dominant. The histories of the sciences reveal that, as more data covering a greater range of materials and environments are analyzed, it frequently becomes necessary to expand and modify theories for the explanation of scientific phenomena. Richey (1942) realized that certain characters do have a multiplicative effect on other characters and proposed that "mock dominance" be eliminated from further consideration in connection with hybrid vigor. Dempster (1943) discusses "mock dominance" further and concludes that though the existence of gene interaction based on certain measures might be relatively insignificant from the standpoint of practical application, it is doubtful whether it should be described as "mock dominance." The purpose of this article is to point out the need for and present an expansion of the theory for the explanation of heterosis.

Any discussion of heterosis of necessity involves a discussion of dominance. This latter term is used by geneticists in two quite different senses. (1) It has been used to denote the degree of expression of one or the other of the two contrasted characters resulting from the action of the heterozygous gene pair (Aa) plus the action of the environment, in which A represents any gene and a its allel. Then, an intra-allelic interaction of A and a may be involved as well as an interaction with the environment. In such studies the genotypes are known or determined, at least in respect to the major gene pair or pairs differentiating the contrasted characters under consideration. Also, the balance of the genotypic complex and the environment presumably have been controlled sufficiently to allow the making of valid comparisons involving the heterozygote Aa and the two homozygotes AA and aa. It is evident that in such studies the material is not limited to the F_1 generation and the two parents, but may include any comparable material in which the heterozygote Aa and the two homozygotes AA and aa can be identified. (2) Also, dominance has been used to denote the degree of expression of one or the other of the two contrasted characters in the F_1 generation as compared to the expression of these contrasted characters in the two parents. The parents should approach homozygosity sufficiently close so that such comparisons are justified. Then, it is apparent that both intra-allelic and inter-allelic interactions may be involved as well as interactions between the genes and the environment. Obviously, under (2) the material is limited to the F_1 generation and the two parents. In this article the use and scope of the term dominance is that given under (1) & (2).

The theory of gene action as developed by Goldschmidt (1938) aids materially in understanding the phenomena of dominance and heterosis. That the genes control rates of reactions (Wright, 1916; Goldschmidt, 1917) is basic to this theory. Other biological phenomena used by Goldschmidt in developing his theory of gene action are thresholds, timing, interrelationships of the different reactions catalyzed by the genes and the numerical systems involved. For a discussion of these phenomena the reader is referred to Wright (1916, 1941) and Goldschmidt (1938). The numerical systems and their relationship to the nature of the interactions of the genes as measured by end products are discussed in more detail by Powers (1939, 1941). These physiological genetic theories basic to an understanding of dominance and heterosis will not be discussed in detail in this article but should be kept in mind while interpreting the data which follow.

To facilitate discussion, data are given in Table 1 for number of ripe fruit per plant, size of fruit and yield of ripe fruit per plant of certain F_1 tomato (*Lycopersicon*) hybrids and their parental inbred lines. An understanding of the relationship existing between the characters is essential to an interpretation of the data: Number of ripe fruit per plant and size of fruit are subcharacters of yield, as the product of number of ripe fruit by weight of fruit (size) gives yield. Any discrepancies noted in the table are due to dropping of decimals in calculating size of fruit.

The data in Table 1 show that the following situations exist as regards the subcharacters number of and size of fruit. The F_1 hybrid 4109 × 4110 shows heterosis for number of ripe fruit per plant and partial dominance for large size fruit. In the F_1 hybrid between 4101 and 4103 more fruits per plant is dominant and size of fruit shows no dominance. Finally, both few fruits and small size are partially dominant in the F_1 hybrid 4102 × 4110. Yet, in all three of these hybrids number of fruit and weight of fruit combine to produce heterosis for yield.

The third situation was found to exist for four other crosses; namely, when 4101 was crossed with 4109 and 4110 and when 4102 was hybridized with 4109 and 4110. Hence, these findings are well established statistically. Also, Powers (1941) in previous investigations found that fewer fruits per centimeter of branch exhibited either complete or partial dominance and that small size of fruit in crosses involving *Lycopersicon pimpinellifolium* (Jusl.) Mill. and *L. esculentum* Mill, was partially dominant. Then, that less desirable characters exhibiting partial dominance may in certain instances combine to produce a third highly desirable character which shows heterosis is well established.

TABLE 1

NUMBER OF RIPE FRUIT, SIZE OF FRUIT AND YIELD OF RIPE FRUIT OF THREE F_1 TOMATO HYBRIDS AND THEIR PARENTAL INBRED LINES

Hybrid or inbred line	Ripe fruit	Size	Yield
	Number	Grams	Grams
4109	118.3 ± 12.91	12 ± .50	1364 ± 151
F_1 hybrid	183.2 ± 13.32	16 ± .68	2876 ± 177
4110	109.1 ± 11.34	17 ± .58	1868 ± 149
4101	4.3 ± .32	119 ± 6.49	513 ± 39
F_1 hybrid	20.5 ± 2.27	89 ± 3.66	1827 ± 196
4103	19.5 ± 2.94	55 ± 2.74	1066 ± 159
4102	4.4 ± .69	138 ± 12.81	607 ± 86
F_1 hybrid	44.5 ± 2.52	55 ± 2.93	2428 ± 150
4110	109.1 ± 11.34	17 ± .58	1868 ± 149

The fact that partial dominance for the smaller of two contrasted quantitative characters occurs would lead one to suspect that the genetic phenomena responsible for dominance and heterosis would produce values less than that of either parent. Two such cases have been reported for mean number of fruit per centimeter of branch. Danmark × Johannisfeuer and Danmark × Red Currant were the crosses for which Powers (1941) found fewer fruits per centimeter of branch to exhibit heterosis.

The inbred lines whose F_1 hybrids (Table 1) showed partial dominance for small number of fruits per plant were selected from crosses involving the three parents, Danmark, Johannisfeuer and Red Currant. Hence, it is not surprising that partial dominance for fewer fruits should occur. The data on average number of locules per fruit for a hybrid involving two of these inbred lines are listed in Table 2.

TABLE 2

Mean Number of Locules Per Fruit

Hybrid	P_1	F_1 hybrid	P_2
4110, P_1 × 4101, P_2	9.6 ± .328	7.3 ± .249	11.7 ± .499

The F_1 hybrid has fewer locules per fruit than the fewer loculed parent 4110. The same was true of six other hybrids from a total of nine which had 4110 as one of the parents. Hence, that this phenomenon does occur is well established experimentally.

Clearly, an expansion of Jones's theory for the explanation of heterosis is desirable. His theory as presented does not take into account the fact that in some cases the effects of the genes are geometrically cumulative. The first part of Jones's hypothesis, namely (1) a large number of genes are responsible for the differentiation of most quantitative characters still holds. The second part, (2) those genes favorable to the production of the desirable quantitative character are at least partially dominant needs to be expanded; because in the cases in which the effects of the genes are multiplicative, those genes not favorable to an increase of the quantitative character may show no dominance or partial dominance and still the character itself may show beneficial heterosis. This statement may be simply illustrated as follows. Assume that number of fruit for the inbred lines 4102 and 4110 are differentiated by an allelic pair of genes AA and aa; and likewise assume that size of fruit is differentiated by an allelic pair of genes BB and bb. Then the genotypes of the parents and F_1 hybrid of Table 1 for the cross 4102 × 4110 would be:

4102	AAbb
F_1 hybrid	AaBb
4110	aaBB

It is evident that the heterosis of the F_1 hybrid for yield (2,428 grams) would be due to the multiplication of the effects of Aa (44.5) by the effects of Bb (55); yet, both Aa and Bb are partially dominant for lower yield. The genotypic situation depicted is probably far simpler than that which actually exists, but it does serve to illustrate that the assumption of partial dominance of those genes favorable to the production of the quantitative character is not necessary when the inter-allelic interactions of the genes are such that their effects are multiplicative. In fact, there may be no dominance or even partial dominance of those genes not favorable to an increase of the quantitative character under consideration and still the character could show heterosis.

In order to understand heterosis, it in necessary to realize that this phenomenon is a phase of quantitative inheritance, the same as are dominance and partial dominance. In reality, as previously pointed out by Powers (1941), heterosis and dominance are different degrees of expression of the same physiological genetic phenomena. This is simply illustrated by the graph of Fig. 1. On the graph the position of the F_1 hybrid determines the type of heterosis or dominance that is exhibited. For example, if the value of the F_1 hybrid falls between 3 and 5, partial dominance for an increase of the quantitative character would be exhibited. That the expression of dominance is dependent upon both the genotype and environment has been demonstrated by a number of workers (Goldschmidt, 1938); and that dominance may be shifted to heterosis or vice versa, by varying either the genotype or environment, has been shown by Powers (1941). Hence, it is evident, as illustrated by the graph, that heterosis and dominance are different degrees of expression of the same genetic phenomena and are dependent upon both the genotype and environment.

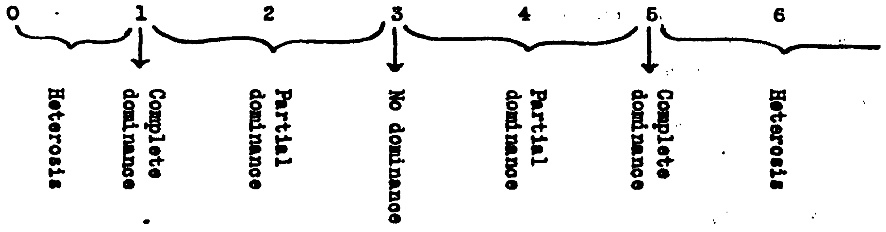

FIG. 1. Values of F_1 Hybrids and Parents in Relation to Heterosis and Dominance.

Before closing the discussion, a matter of terminology should be mentioned. Many plant breeders and geneticists have become accustomed to associating heterosis with the beneficial or more desirable character. There seems to be no genetic reason for making such a distinction. However, in plant breeding sometimes a distinction is desirable. Therefore, rather than coin any new terms to fit the genetic interpretation given here, it is suggested that the term heterosis be employed in the usual sense and non-beneficial heterosis be employed when the F_1 hybrid exhibits heterosis for the less desirable of the two contrasted characters.

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TRANSPLANTATION AS A TOOL OF DEVELOPMENTAL GENETICS

THE transplantation technique has been of inestimable value in many fields of experimental biology, especially in the analysis of embryonic induction and in the study of endocrine relationships. In the rapidly growing science of physiological genetics there will undoubtedly be many problems which can be approached by transplantation methods. In fact, some important advances of this kind have already been made. There is sufficient reason, then, to call attention to limitations inherent in these methods and which must not be lost from sight if confusion is to be avoided.

The ultimate question of interest to the physiological geneticist is, of course, that of gene action. In this respect we can not look for unequivocal information from transplantations. For, even in the relatively simple cases in which traits are determined by diffusible substances and even if the production of these substances appears to be limited to certain parts of the organism, no satisfactory solution of our problem is afforded by the assumption that the elaboration of the diffusible substance is virtually identical with the activity of the gene in question.

If we except the apparently rare occurrence of the elimination of definite chromosomes in the developmental history of certain organs, it must still be assumed, any evidence to the contrary lacking, that all genes are distributed to all cells of the body. The problems of differentiation will not be solved by the *ad hoc* assumption that genes have been lost from certain parts. All biological experience speaks against the justification or general validity of such an hypothesis. There is a definite possibility, to be sure, that cytoplasmic differentiation curbs or modifies the activity of certain genes in specific parts, but we have at present no factual evidence whatever in support of this assumption.

Even if the experimenter's question relates only to the problem of the determination of certain hereditary features within a single organ the transplantation technique can not always be expected to give a definite answer. This is to be illustrated here with reference to recent experiments by Gayer and Hamburger (1943) on material of Creeper fowl. In earlier experiments Gayer (1942) had demonstrated that eye anlagan of genetically normal chicken embryos, when transplanted to the flank of genetically normal hosts, generally show in later stages abnormalities which are very similar to those typical of intact late homozygous Creeper embryos. It was clear, therefore, that "phenocopies" of all essential features of homozygous Creeper eyes could be produced by the simple expedient of transplantation to an unusual locality. In their new and beautifully executed experiments Gayer and Hamburger (1943) were able to show that the orthotopic transplantation of normal eye anlagen (including surrounding tissues) to normal hosts leads in most cases to the development of entirely normal eyes.

On the basis of these new observations Gayer and Hamburger (1943) set out to find an answer to the following alternative questions: "Does the Creeper factor, in doube dose, in producing its effects on the eye, act locally, starting in the cells of the eye primordium itself; or indirectly, starting in structures outside of the eye, and transmitting its effects by way of inductions or similar mechanisms?" The fact that normal eye anlagen transplanted orthotopically develop into normal eyes was assumed to provide the basis for "crucial" tests.

What were the results? (1) Many transplants of homozygous Creeper (CpCp) primordia developed entirely normally within *genetically normal (cpcp) hosts.* This, the authors admit, "gives no crucial answer." For, "it can be explained either by assuming that the transplant was deficient, and the deficiency was remedied by the cpcp milieu ——, or by assuming that the transplants had no intrinsic deficiencies at all." (2) Transplants of CpCp eye primordia to cpcp flanks in subsequent development produce the typical features of homozygous Creeper embryos. This result is again, and rightly, dismissed by Gayer and Hamburger (1943) as "not crucial." For, "one may argue that the flank region of the cpcp host, in contrast to the head region, does not provide for an adequate supplementary agent, at least not in the necessary quantity." (3) A single instance is recorded in which a homozygous Creeper embryo bearing an orthotopic transplant of a normal embryo survived sufficiently long to diagnose the condition of the eye in the transplant. The eye showed abnormalities similar to those of the host, but less extreme. The following features are worthy of note. "The transplant eye is larger than the host eye." The coloboma of the transplant eye is "of lesser extent," "the retina duplication only along one margin of the choroid fissure," and there was in certain parts of the sclera an "abnormally thick cartilage layer." Gayer and Hamburger (1943) think this case tends to confirm the interpretation that the typical coloboma of homozygous Creeper eyes "is imposed on a potentially normal eye by factors located in the phocomelic head." They are forced to admit, however, that "the validity of this case is weakened by the following considerations. The host head as a whole is abnormal and misshapen, and it is conceivable that the eye abnormalities are due to this condition," and they call attention to the fact that the same abnormalities had been produced by Gayer (1942) in genetically normal eyes by transplanting them to an abnormal environment, *viz.*, to the flank. In our opinion, it would be impossible to draw valid conclusions even if further experiments of the same type should yield similar results, and even if such results were obtained in the absence of other head deformities; for it is difficult to see why the argument which Gayer and Hamburger (1943) used in the interpretation of their results with transplants of CpCp eye primordia to cpcp flanks (quoted above) should not apply to this situation as well, or why, in fact, it should not apply to the results of transplanting normal primordia to the flank of normal hosts.

Such are, briefly, the results of the experiments. The conclusions which the authors draw are definite and unequivocal: "(a) The deficiencies are not due to 'local gene action' in the eye primordia. The Cp-factor, in producing these deficiencies, operates in an indirect way. The primary action is on structures extrinsic to the eye. (b) Whereas CpCp embryos are non-viable, CpCp eye primordia not only survive in orthotopic position but they show no effect of the CpCp-genotype which they carry in each of their nuclei."

To us, on the other hand, it seems that all the results can readily be interpreted in quite another fashion. Let us make the following assumptions: (a) a substance x is normally elaborated by all embryonic tissues and cells or by certain types of cells occurring throughout all tissues; (b) the elaboration of substance x is hindered by abnormalities in the supply of oxygen or certain nutrients; (c) substance x is needed for cell multiplication and/or certain steps of differentiation; (d) substance x can, if necessary, be taken up by cells from the blood or from neighboring tissues; (e) the rate of production of substance x is reduced in the presence of the Creeper mutation.

These are scarcely unusual assumptions or ones which are unlikely to occur. If such conditions should actually prevail, what results could be expected in the various situations which underlie the experiments of Gayer and Hamburger (1943)? The eye abnormalities of late homozygous Creeper embryos would, of course, be expected by definition. In the case of cpcp transplants to the flank subnormal conditions of circulation might be anticipated to result in the phenocopies which were found. Either the same argument or the intrinsic conditions of their Creeper nature would apply to CpCp transplants to the flank of cpcp embryos. In cpcp eye primordia orthotopically transplanted to CpCp embryos it might again be the unfavorable conditions after transplantation which prevent the anlage material from producing a normal eye. On the other hand, either cpcp or CpCp eye primordia transplanted orthotopically to cpcp heads might develop normally on account of sufficient supplementation reaching the transplant in this location and, in the case of CpCp transplants, thereby overcoming intrinsic deficiencies. If these arguments hold for the morphological eye abnormalities (coloboma, etc.), they can be applied *a fortiori* to growth of the eye.

It is not our intention to assert that the assumptions which have here been made actually exist under the conditions of the experiments which have been discussed. But we do wish to point out that the transplantation experiments of Gayer and Hamburger (1943) are quite incapable of differentiating between conditions, such as would exist under our assumptions and the developmental situation actually postulated by them on the basis of their results.

Development of the normal eye may be referred to as "non-autonomous," if judged by the fate of heterotopic transplants; it may be looked at as "autonomous" in view of the results of orthotopic transplantation. The two designations are descriptive of each particular set of circumstances rather than explanatory of underlying causes. It is similar with the eyes of homozygous Creeper embryos. To put it into cruder terminology, the fact that a "diseased" part remains abnormal in a "diseased" organism, but becomes healthy in a favorable environment neither proves nor disproves that the part in question was not, to start with, in a pathological condition.

The conclusions at which Gayer and Hamburger (1943) arrived, as far as reference has been made to them by us, constitute one possible explanation of the established facts. They are no more than a hypothesis, however, and evidence of a different nature will be needed to verify whether or not these particular suppositions represent the correct explanation.

Situations similar to the one which has been discussed here will undoubtedly arise often in the developmental analysis of genetic traits. It was our purpose to show that transplantation experiments will not always be capable of providing conclusive information and that, in any event, great circumspection must be exercised in the interpretation of their results. Such caution will probably be particularly necessary whenever in the analysis of hereditary variations there is a possibility that partial or complete suppression in the elaboration of diffusible substances or alterations of their chemistry may play a role.

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SELF-FERTILIZATION IN THE RUSSIAN DANDELION, *TARAXACUM KOK-SAGHYZ*

THE Russian dandelion normally is self-sterile and sets seed sparingly, if at all, when protected against cross-pollination by insects.[1, 2, 3, 4] During the past year and one half, an opportunity was provided for further observations of self-fertility and self-sterility in this species, on greenhouse plants being grown for studies in cytology and rubber content.[5] These observations indicate a wide variability in extent of flowering and self-fertility, apparently associated with the season.

Seeds were sown in seed pans on May 16, 1942. A month later, between 800 and 900 seedlings were transplanted into 3-inch pots; these were later transferred to 4-inch and 5-inch pots as required. All plants were given liquid organic fertilizer from time to time and thus kept in a growing condition, although many became pot-bound before the end of the study. The greenhouse was heated during the winter, and a night temperature of between 55° and 65° F. and a day temperature of between 65° and 75° F. was maintained. Summer temperatures in the greenhouse were generally somewhat higher than those prevailing out of doors. No artificial illumination of any sort was given. The greenhouse was screened, and thus was free from insects.

On August 16 the first plant came into flower, and others followed intermittently throughout August, September and October. Of the hundreds of blossoms produced by a score or more of plants which flowered during August and September, only one head, containing four seeds, was set. Numerous hand-pollinations were made by rubbing together two blossoms from the same plant. None of these produced seed; although similar pollinations between two different plants produced the normal set of 40 to 80 seeds. *T. kok-saghyz* is obviously highly self-sterile under these conditions.

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[1] V. Poddubnaja-Arnoldi and V. Dianowa, *Planta*, 23: 19, 1934.

[2] V. A. Koroleva, *Soviet Plant Ind. Record*, 2: 1, 1940. (Translation No. 21, U.S.D.A. Rubber Plant Investigations.)

[3] H. E. Warmke, *Bull. Torrey Bot. Club*, 70: 164, 1943.

[4] H. A. Borthwick, M. W. Parker and N. J. Scully, *Bot. Gaz.*, 105: 100, 1943.

[5] This work was undertaken in cooperation with the Rubber Plant Investigations Project of the Bureau of Plant Industry, Soils and Agricultural Engineering, U. S. Department of Agriculture.

Further observations on flowering and seed setting were arbitrarily limited to a group of 382 representative plants. The data collected from this group of plants are shown graphically in Fig. 1. A total of 159 plants, or nearly 42 per cent. of the total, flowered between the middle of August and the end of the following May. Two maxima are evident: one in November, when 66 plants were observed to flower, and another in April, when 50 plants came into flower. These maxima are separate and distinct, because during the latter part of December and all of January and February few new plants came into flower and those that had flowered earlier returned to a vegetative state. This would seem to indicate an inhibition of the flowering response during the middle of the winter, even though conditions were such that vegetative growth continued.

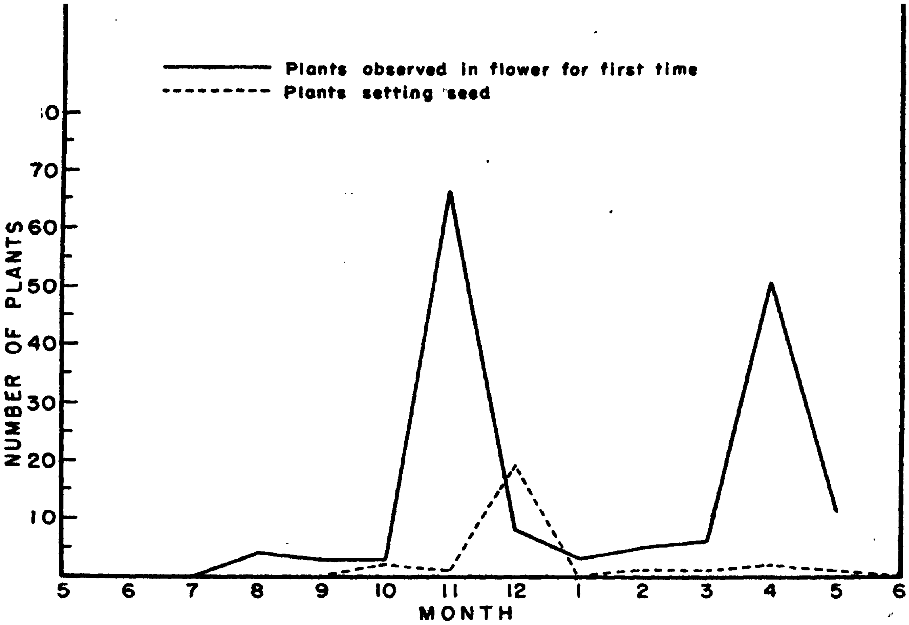

FIG. 1. Flowering and seed record of 382 greenhouse plants of *T. kok-saghyz*. Three maxima are evident: two in flowering (November and April) and one in the number of plants setting seed by self-fertilization (December).

Flowering records were discontinued on June 1, but seed records were continued until July 1, when the plants were transplanted out of doors and all record taking was discontinued. The rapid decline in new flowering during May, however, probably indicates the onset of a summer dormancy, previously observed in this species by others workers.[6, 7]

The broken line in Fig. 1 records the number of plants from which mature seeds were harvested during the course of the observations. A pronounced peak in seed setting is observed in December, following the outbreak of flowering in November. No such peak is observed following the April flowering maximum. During October, November and December seeds were collected from 22 (26.2 per cent.) of the 84 plants which had flowered up to that time. This is in sharp contrast to the five plants (6.7 per cent.) which set seed among the 75 plants that came into flower between January 1 and the end of May. The yield of seed, also, was greater in the winter than in the spring. The 22 fall- and winter-flowering plants from which seed was harvested set 53 heads with a total of 1,690 seeds, or an average of 31.9 seeds per head and 76.8 seeds per plant. The five plants which set seed during the late winter and spring produced six heads with a total of 110 seeds, or an average of 18.3 seeds per head and 22 seeds per plant.

The causes for the flowering maxima in November and April and for the high percentage of seed set in December under the above conditions are not clear. Since the experiment was not planned as a study in temperature and photoperiod, no conclusions are legitimate beyond the simple observations that the flowering maxima occur at approximately the onset and the end of the cold season, both on relatively short photoperiods (one decreasing and the other increasing), and that the high set of seed in December may possibly be a sort of "end-season fertility," a phenomenon commonly observed in *Nicotiana*[8] and other self-sterile species. Borthwick, Parker and Scully,[9] in a series of controlled experiments, have indicated the importance of low temperature in the induction of flowering in this species.

Since the development of an unreduced and unfertilized egg is characteristic of the polyploid members of the genus, it seemed

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[6] V. A. Koroleva, *Soviet Plant Ind. Record*, 2: 1, 1940. (Translation No. 21, U.S.D.A. Rubber Plant Investigations.)

[7] G B. Neiman and A. A. Sosnovets, *Dok. Veses. Akad. S. Kh. Nauk im Lenina*, No. 2: 15, 1941. (Translation No. 703, U.S.D.A. Soil Conservation Service.)

[8] E. M. East and J. B. Park, *Genetics*, 2: 505, 1917.

[9] H. A. Borthwick, M. W. Parker and N. J. Scully, *Bot. Gaz.*, 105: 100, 1943.

possible that this rather abundant seed setting in the absence of insects might have been apomictic—in spite of the fact that *T. kok-saghyz* has been shown normally to reproduce in a sexual manner.[10,11] To determine the nature of the process by which the seeds were produced, a study of the characteristics of the offspring was made. Since the original Russian stock was highly heterozygous, as indicated by wide variation in habit and leaf characters, the offspring of any given plant should show genetic segregation if they result from sexual self-fertilization. If the offspring are the result of apomixis, they should be much more uniform in appearance.

Four hundred and sixty-three offspring were obtained from the seed of uncrossed heads of 15 different plants. These were observed until they were nine months of age, at which time many had flowered. The variability among the offspring from a given plant was nearly as great as in the original Russian stock: some leaves were large, others were small; some leaves had entire or nearly entire margins, while others were deeply incised; some had considerable color in the midrib, while others were colorless. Such extensive variation can hardly be thought of as the result of environmental influences; it points strongly to genetic segregation and thus to true sexual self-fertilization.

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[10] V. Poddubnaja-Arnoldi and V. Dianowa, *Planta,* 23: 19, 1934.

[11] H. E. Warmke, *Bull. Torrey Bot. Club,* 70: 164, 1943.

THE
AMERICAN NATURALIST

VOL. LXXVIII *July–August, 1944* No. 777

CONCEPTS OF HOMOLOGY AND ANALOGY[1]

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ALAN BOYDEN (1943) has done biology a good service by reviewing the history and the conceptual significance of the terms homology and analogy. Having arrived at somewhat different conclusions and other viewpoints in going over much the same ground in 1926 and 1937 (unpublished reports), I venture now to enter the discussion.

EVOLUTION OF THE HOMOLOGY CONCEPT

With abounding respect for the master anatomist, Boyden recommends that we return a full hundred years to Richard Owen's pre-evolutionary concepts and definitions of homology and analogy. This recommendation obviously did not stem from any belief that the law of priority holds for concepts, but rather from Boyden's conviction that Owen's 1843 definitions remain precise, clear and adequate. That, they indeed were, in Owen's day. But the ideas of homology and analogy have evolved through a century of vast advances in biology, so that it is now difficult in some respects to trace the homology of ideas. During the same period most of the major concepts of biology have become fundamentally modified. Think of "evolution," of "mutation," of "species."

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[1] For their kindness in reading a semi-final draft of the manuscript, and in offering constructive criticisms, I am greatly indebted to Drs. William K. Gregory, Ernst Mayr, Charles M. Breder, Jr., Francis B. Sumner, A. Franklin Shull and Lee R. Dice, as well as Dr. Boyden. A number of suggestions thus received have been incorporated in the paper, but I do not imply that any of my helpful colleagues agrees completely with my views.

The homology concept has undergone a great, but not yet complete change, from static to dynamic. Traditional meanings and limitations have held on, at times with the effect of confusing ideas and retarding progress.

In its original form the homology concept pertained only to structures, as they are independently manifested in the adults of different animals (or plants). It called for correspondence in position, in agreement with the mathematical concept of homology, and for similarity in fundamental structure. Owen's idea of agreement in position and structure, indicating "the same organ in different animals under every variety of form and function," anticipated the theory of common descent with modification, and took on vastly greater significance as the theory of evolution became the dominant interpretation of biology. As a result the homology concept became and has ever since remained a potent one in evolution, and also in embryology and in modern systematics, as well as in comparative anatomy.

Homology has thus come to signify an agreement in evolutionary derivation, and, either as a corollary or as a prime criterion (Haeckel), an agreement also in embryonic development. Proof of homology has become the basis of phylogeny. The ideas of homology and community of origin have become intimately associated, almost to the point of synonymy. This association has perhaps gone a bit too far, for fundamental agreement in structure and in mode of ontogenetic origin does not always involve a common phyletic origin. We will revert to this point later (p. 300).

PERTINENCE OF HOMOLOGY TO FUNCTIONS AS WELL AS STRUCTURES

The original limitation of the homology concept to structures has been most unfortunately persistent. Acceptable only from the standpoint of static morphology, this limitation is undesirable in its effects and illogical in the modern view: undesirable, because it maintains an overemphasis on structure as a tool of evolutionary and taxonomic research; and illogical, because systematists and geneticists are dealing more and more with physiological as well as morphological characters and because biologists have come to recognize the inseparability of structure and function. Conklin (1943: 105) well expresses the current viewpoint: "No postulate of biology is more certain than this, that the functions of life are inseparably associated with the structures of living matter. This is a conclusion of the utmost importance in biology and philosophy."

Since homology has become a basic evidence of evolution, its continued limitation to structures seems incongruous. It is common understanding that function and structure yield like evidence regarding relationships and ought to be considered on the same terms.

It is recognized, to be sure, that functions are repeatedly subject to convergent evolution, both progressive and degenerative, but all biologists would now agree that this is also true of structures. Superficial likenesses in functions—mere uses—often arise independently, but so also do superficial resemblances in structures. In either case we deal with analogies rather than homologies. Fundamental similarities in the "intrinsic functional mechanism" are properly regarded as a criterion of homology (Tait, 1928)—as valid a criterion as that furnished by deep-rooted agreements in structure. Tait clearly detailed the fundamental similarities in the physiology of homologous organs, particularly those of internal secretion (but of course went too far in insisting that homologous organs never change their intrinsic functions; consider, for example, the modification of the anal fin in the males of poeciliid fishes to form the intromittent organ). The problem of the homology of certain organs may therefore be subjected to physiological test.

Along with the associated structures, functions having as their chief attribute use rather than biochemical properties may also be indicative of homology. Thus the reflexes and behavior patterns responsible for the flight of two birds possess an evolutionary significance directly comparable to the structural agreement or homology that exists between the wing of the first bird and the wing of the second. The clawing of a cat and of a tiger has much the same meaning as does the homology of the claws. Clawing may be independently evolved, and so may claws.

It is high time that we think and write of homologous functions in the same way that homologous structures have been treated, and that we discard from the definition of homology any necessary restriction to anatomy. Many biologists, I am sure, have thought in such terms. Certainly developmental homologies are conceived in terms of genetically consistent processes quite as much as in terms of the structure, either of the genes or of the final product. And surely every finished organ involves functions just as much as it does structure.

The limitation of the homology concept to structures is perhaps more a function of the stated definitions than of thought, but the definitions do have an effect on concepts and applications. Some biologists whom I have consulted seem surprised or confused at the limitation expressed in recent definitions. As an apparently fair sample we may take the biological definition of homology in Webster's New International Dictionary (second edition):

> Correspondence in type of structure between parts or organs of different organisms due to differentiation by the process of evolution from the same or a corresponding part or organ of some remote ancestor; also, true correspondence in type of structure between different parts of the same individual. Distinguished from *analogy,* or resemblance in function (or sometimes also in form) between organs of different origin.

Though the modern evolutionary meaning of homology is given full emphasis in this and similar definitions, we still find the limitation to structure. Perhaps the next revision will read, "structure or function."

ATTEMPTED RESTRICTIONS OF THE HOMOLOGY CONCEPT

Boyden would have us divest homology of its expanded meanings, and in particular urges that we dissociate "serial homology" (for which he in part adopts Owen's little-used term, "homotypy") from "true or special homology." Boyden stresses the claim that correspondences in structure are much closer in special homology than in "homotypy," illustrating his points by a comparison of the appendages of two crustaceans, *Homarus* and *Callinectes*. Further consideration, however, shows that serial homologs are often much more alike than are some special homologs. Thus pereiopods 2 and 3 of the lobster are more similar to one another than either one is to the corresponding leg of the blue crab. As a whole the lobster's pereiopods are terete; the blue crab's, compressed. In some crustaceans all the walking appendages are short; in others, greatly elongate. Such resemblances in serial homology are presumably due to a common genetic basis and may therefore be used (contrary to Boyden's claim) as evidence in phylogenetic research; they surely have the same sort of evolutionary significance that other types of homology furnish. Broadening comparisons, we often find vastly greater correspondence in anatomy, and in homology, between serial structures in one individual than between the "same" structures in two animals. Thus we see vastly greater agreement in fundamental structure and relationships of parts when we compare the fore limb and the hind limb of a horse, than we do when we contrast the fore limb of the horse with its special homolog, the pectoral fin and girdle of a teleost fish.

It seems unwise to restrict the homology concept to special homology, that is, to the relationship between specifically corresponding structures of different individuals. The wisdom of the broader concept becomes especially clear when we consider the homology between structures which are dispersed at random, or which form elements of a pattern, in which few or none of the individual elements can be homologized with individual elements in another animal. Take scales, for example. It would be a slap at almost any basic concept of homology, to deny, on some arbitrary distinction, that any scale of one teleost, say a trout, is homologous with any scale of another teleost, for example, a herring, even though no one scale over the general body surface of a trout can be specifically homologized with any one scale on the herring. More definite homologies arise when certain scales, associated with fins and with head structures, become particularly specialized. Such scales include the elongate pelvic axillary scale in many fishes, the non-imbricate scale on the top of the head in cyprinodont fishes, and primitively, the scales which in early fishes became modified to form particular membrane bones. Special importance is attached to the homologies between these particularized scales, but there is significance also in the general homology between the non-placoid scales of certain types, and in the lack of homology between placoid scales and cycloid scales.

It seems even more illogical to restrict the concept of homology to structures in different individuals. If we admit the homology between any scale x of an individual trout and any scale, say y, of a salmon, and between this scale y in the salmon and scale z in the trout, then how can we logically deny that homology exists between scales x and z on the body of the same trout?

Considering the original structure of scales leads us to question again the advisability of excluding correspondences in serially segmented structures from the scope of homology. All non-placoid scales seem to possess at least a generalized homology, although in evolutionary origin they are to be interpreted as segmental structures, that is, as articulations in the hardened exterior of each myomere.

Peter (1922) went so far as to urge that the homology concept be restricted to structural agreements between species and higher groups, disregarding the similar structural correspondences between individuals of one species as well as the homologies between parts of the same individual.

The idea has even been suggested that the concept of homology should be applied only to the broader correspondences between the larger groups of organisms. But the principles of phylogeny which pertain to the greater divisions hold in large part for the lesser groups, such as species and genera. Furthermore, there is quite as much need for interpreting homologies between the diagnostic characters of the minor groups as there is for interpreting the evolutionary relationships between the characteristics of the major groups.

Many abortive attempts have been made to narrow the homology concept. The great biological theorist Ernst Haeckel was one of the first to attempt a restriction of the term homology to correspondence between structures of two individuals. For the equivalence of structures in the same organism he concocted two new terms, "homodynamy," applying to structures appearing serially in successive metameres of the body; "homonymy," for structures aligned along secondary axes of the body. So far as I know he proposed no term to cover the generally underemphasized relationship between structures, like hair or scales, that are more or less diffusely distributed over the body. Later, Spemann (1915) proposed that the abandoned term "homonymy" be applied to these relationships between diffuse structures. Richard Hertwig used the term "homonomy" in the sense in which Haeckel had employed "homodynamy"; Gegenbaur followed Haeckel's usages, except that he adopted the spelling "homonomy" in place of "homonymy" and expanded the concept to include the relationships of serially arranged structures within one portion of the main axis of the body.

In one of the better known attempts to restrict the homology concept E. Ray Lancaster (1870) regarded as truly homologous, or "homogenetic," only those corresponding structures which can be traced to a single representative structure in some common ancestor. In contrast, similar structures that result from the action of like forces were called "homoplastic." At first Lancaster restricted the application of the term "homoplasy" to comparable modifications of similar and generally homologous structures. In this sense homoplasy would correspond fairly well to the relation between "independent homologies" (p. 300). But later he expanded the concept to apply to changes resulting from the action of like forces on any structures, whether homologous or nonhomologous. In the end, therefore, Lancaster merely substituted "homogeny" for special homology and "homoplasy" for analogy. His idea of "homogeny" was akin to Haeckel's early concept of "homophyly."

The fact that biologists in general have not adopted such terms and have not followed such rather arbitrary distinctions suggests that neither the terms nor the distinctions may be of much value. The concept of homology has remained a broad one, as indeed it should.

In arguing for the unity of the homology concept I am not opposing the idea of classifying the types of homology. There would be many advantages in the fabrication and use of such a classification, but it would seem wisest to call all the types homologies, specifying the kinds by adjectival prefixes.

Inconsistencies without end would arise from the application of suggested restrictions of the homology concept and of the associated terminologies. Thus, according to some, my left arm is not homologous with my right arm, nor is the left pectoral fin (and girdle) of a fish the homolog of the right fin of the same fish, although my left arm is homologized with the left pectoral of the fish. What some of the concept splitters would have done with diffuse structures like scales, or with resemblances between the successive proglottids of a tapeworm or the segments of an annelid is hard to guess. Would they homologize parapodia or nephridia only in segments that are demonstrably of specific common origin?

If we should consistently exclude right-left, serial and diffuse structures from the homology concept we would ignore many fundamental agreements (*i.e.*, homologies) in phylogenetic and ontogenetic development. To restrict homology to organs or parts that have a specific common ancestral structure would assume modern meaning only if specific sets of genes could be shown to be specifically responsible for the independent development of each structure—which of course would be contrary to the present conclusions of genetics.

It seems to me that the only serviceable modern concept of homology is that of the essential genetic agreement of structures and functions in evolutionary derivation and in embryonic development.

Complexities in Homology

On this or almost any other broad concept homologous relationships involve many complexities. In the first place, there may be many degrees of specificity in homology. Two characters may be homologous from one point of view but non-homologous from another viewpoint. As units of organic structure all cells are homologous, but as units of hepatic tissue, only part of the cells of one animal are homologous with those of another individual. As a vertebrate limb a bat's wing is homologous with a bird's wing, though as a wing it is only analogous. As basic elements of the exoskeletal armor each membrane bone in the skull possesses a generalized homology with every other membrane bone and with each non-placoid scale, just as any ordinary scale is homologous with any other scale (of the same or another individual); but any one membrane bone can be rigidly homologized only with the same bone in another individual (or with a bone on the opposite side of the same animal). By general agreement the teeth of all vertebrates from elasmobranch to mammal are homologous with all denticles on the body surface of any elasmobranch, but as a tooth, any vertebrate tooth is homologous only with other teeth. As a certain type of tooth, the mammalian molar, to cite an example, is homologous only with other true molars. Individually specialized molars are homologous only with the corresponding tooth in another mammal or on the other side of the jaw in the same individual. Where to draw the line in interpreting homologies is a function of the special needs in any comparative study. It is not logical, however, to exclude from the homology concept any structures which have a true agreement in derivation—of the degree and sort indicated by the comparison being made.

Many complexities in homological relationships come to mind when we review the facts of anatomy and variation. Thus the membrane bones shift from the exoskeleton to the endoskeleton, to become covered by unmodified scales; when accessory scales are developed, the homologs come to lie three deep. Similarly, the lepidotrichial elements of the fin rays take on new structural relationships and to this degree outgrow their basic homology with scales; like membrane bones, the fin rays may become covered with ordinary scales. Nature's faculty for overriding regular rules is exemplified by the development of a new pair of horns alongside the old pair in four-horned goats and sheep; also by homeotic variations; and by the almost identical modification of non-homologous structures. Such irregularities, however, encumber almost all biological concepts, but destroy neither their validity nor their usefulness.

Perhaps even more serious difficulties beset the homology concept when we try to express homologies in terms of genetics. Individual genes have multiple effects, and a given character may be affected by many genes. Similar results may be effected by different genes or combinations of genes. Mutations greatly modify the genetic mechanism. Modifying genes come and go. Some homologous mutations are virtually identical in fundamental nature and in effect; others are more or less different. "Systemic mutations" (Goldschmidt, 1940), which greatly reorganize the hereditary complex, are not to be wholly excluded. What degree of genetic integrity is to be required for the interpretation of homology? How complete must the genetic analysis be, to warrant such interpretation? In many cases how can we feel any assurance as to the fundamental agreement of corresponding structures, in terms of the genetic mechanisms involved? Some geneticists have gone so far as to decry the significance of homologies, but Boyden (1935, 1943) has plausibly refuted such destructive views and has indicated that homology may still be regarded a genetic phenomenon.

Boyden (1943) stresses the increasing uncertainties that pertain to homological interpretations, as we shift our attention from forms capable of interbreeding to those progressively less closely related. I feel inclined to emphasize the special difficulties that arise in interpreting the homologies between the characters of very closely related forms. In the first place the genetic background within minor circles of evolution must be greatly complicated by the processes of reticulate evolution (stressed by Dobzhansky, 1941, and by Huxley, 1943). In the second place the frequency of parallel evolution among related forms—attested by a great mass of speciational evidence—often makes it impossible to decide whether or not detailed agreements are due to common origin. How then can we objectively interpret the homology of such characters? Homologies in phylum, class, order and family characters are commonly much more obvious and secure than are the homologies in generic, specific and subspecific characters.

Still further complications arise when we try to reconcile the facts of experimental embryology and regeneration with the homology concept. The regeneration of an antenna in place of an excised eye in crustaceans has long been a puzzle from the viewpoint of homologies. Knowledge of organizers, fields of growth and of differentiation, of axial gradients and of other developmental phenomena interposed between the gene and the specific adult, can hardly be said to have simplified the concept of homology. These considerations force us to treat homology with less extreme precision than was once demanded. For example, the third anal ray of the adult male in poeciliid fishes, such as *Gambusia,* has certain highly characteristic structural modifications. These same features appear on the fourth ray, if the third ray during development be excised at the base (Turner, 1941). Under these conditions the field of differentiation can operate on the fourth ray. We are finding that these and other gonopodial features in the poeciliids seem to owe their expression to position: structures normal to the anterior edge of the gonopodium normally develop there on ray 3, but will appear on ray 4 if that ray forms the front margin; other special structures that normally develop on the posterior edge of ray 4 or of ray 5 will develop on other rays if these rays by reason of malformation or operation present a free posterior edge. Obviously, such characters do not arise *de novo*. They may surely be regarded as homologous with the normally manifested structures, though they appear on new parts (different rays) or in duplicate (on two or more rays instead of one).

Transformation of one type of structure into a distinct type may occur in the process of normal development as well as in regeneration. A noteworthy example is the change with age of the third anal ray in certain fishes, for example *Mugil* (Jacot, 1920: 207–208), from a flexible, articulated, bilaterally paired soft ray into a robust, bony, pungent, non-articulated, solid spine. It is doubtful that spines are homologous with soft rays, except in a very general sense, yet here we find what appears to be a true spine developing out of a soft ray. The field for spine formation appears to move backward far enough to involve an additional ray. The transformed structure is surely not a *de novo* development. It must result from the same developmental factors as other spines. It is therefore more closely and certainly homologous with the other spines than with the soft ray out of which it was transformed.

INDEPENDENT HOMOLOGIES

Ineradicable complexities seem to be inherent in certain relations which perfectly fit Owen's concepts of homology but do not completely qualify under the evolutionary concept of homology. For many years such relations have perturbed students of evolution. They were apparently prominent in Lancaster's mind when he first (1870) proposed the term homoplasy to designate the similar but independent modification of homologous structures. Referring to the independent origin of morphologically similar cusps on homologous teeth of different mammals, Osborn (1907) concluded that we "deal with homology, or more strictly with a *principle intermediate between homology and analogy.*" We can find, in fact, a full transition between homologies and analogies.

Detailed analyses in systematics, in comparative anatomy and in animal behavior often reveal examples of the identical but independent modification of homologous structures or behavior patterns. There may be full agreement in all morphological or behavioristic relationships and in ontogeny. In such circumstances all criteria of homology may be met, except that of a single, continuous lineage. Good circumstantial evidence indicates, to take one example from our own studies, that bifid teeth and intestinal coils of a certain type have been evolved repeatedly in the Goodeidae, a family of cyprinodont fishes (Hubbs and Turner, 1939). In the Clupeidae, as a second example, a peculiar type of raker-lined pocket has been developed, again and again we feel sure, by an extension and evagination from the upper anterior end of the fourth gill-slit (Hubbs and Lagler, MS). The end results of such parallel evolution may be scarcely distinguishable on any morphological, physiological or developmental grounds. Are they homologous? On the basis of essential similarities and of mode of development in the individual we may answer "Yes"; on the basis of monophylety, we could say "No." I prefer to compromise by calling such relations "independent homologies," despite the apparent contradiction in the term. Some may care to use a special term for such relations, and perhaps will choose "homoplasy" (employing Lancaster's term in the original rather than the modified definition—see p. 295), or "homomorphy" (Fürbringer, Gegenbaur), or "rectigradation" (Osborn, 1907). The fundamentally important general consideration is to recognize that conditions intermediate between homology and analogy exist. In each case the significant things are to understand the relations involved, to make clear what doubts or unsolved interpretations remain and to specify what is meant by the terms used.

The same or a similar modification of homologous attributes may occur on convergent or divergent as well as on parallel lines of evolution, and in distantly as well as in closely related groups. Evidence keeps accumulating, however, to indicate that such independent homologies are particularly characteristic of closely related lineages. Intrinsic as well as extrinsic factors are probably responsible for this circumstance. In related forms homologous genes are apt to develop homologous mutations. Certain physical or chemical features in the genes or in the constitution of the organism may predispose toward a given modification. Peculiar environmental relations, or evolutionary steps already taken in a certain direction, may give special advantage to a certain type of change. Finally there is the still unproved and inherently improbable though often asserted innate tendency to vary in a certain direction.

When the homologies or seeming homologies are within one evolutionary circle, it is often difficult or impossible to tell whether they arose monophyletically or polyphyletically. If the similar characters are polyphyletic in origin, in terms of time, they may or may not be the result of homologous mutations. But the precise genetic mechanism will seldom be known and will rarely be exactly identical. The more precisely we fix the prerequisites for the recognition of homology, the more difficult may the appraisal become. But the need for the best possible appraisal will remain.

In one sense almost all homologies are independent. In the most rigid interpretation a continuity between characters can occur along only those lineages which are maintained by certain types of asexual reproduction.

The complete turn-over of genes in each generation of sexually reproducing animals creates a minor discontinuity. A slightly greater discontinuity results when gene-determined characters skip one to many generations. Some characters, such as those which owe their expression to rare homozygous recessives, may appear very rarely. Still less frequent in expression may be characters that arise from independent homologous mutations. Characters which appear to have been totally lost for geological ages may still be represented by a hidden reserve of unexpressed genes. This becomes evident when we consider exceptions to Dollo's law of irreversible evolution, for instance, the reappearance of teeth in one isolated genus of anurans (Cornman, 1943). The development of ctenii on one highly specialized genus of poeciliid fishes may furnish another example. Surely the occasional reappearance of long-lost characters does not represent *de novo* development. Just what degree of genetic continuity is to be required for the identification of characters as homologous? Trouble lies in store for those who attempt to fix too precise limits, even when the genetic mechanism is thoroughly understood. Precision in concepts should not transcend the complexities that exist.

CONCEPT OF ANALOGY

Boyden urges that we return also to Owen's concept of analogy—but Owen like almost all subsequent authors seems to have wavered in his view as to whether analogy applies to all structures exhibiting like function or only to essentially unlike structures with one function. Owen's initial 1843 definition of "analogue," as quoted by Boyden, namely "a part or organ in one animal which has the same function as another part or organ in a different animal," would seem to exclude "homologues," which in contrast were defined, in the static view of pre-Darwinian time, as "the same organ." It seems probable that Owen first meant to apply the term analog only to organs that are not homologous. In 1848, however, as Boyden demonstrates by a quotation, Owen admitted that homologs like the pectoral limb of porpoise and fish may also be analogs. It is to Owen's later or 1848 concept that Boyden would have us return.

The concept of analogy, like that of homology, has undergone changes with time. When with the acceptance of the evolution doctrine the basic significance of homology became that of agreement in origin and descent, the concept of analogy, by dictates of contrast, came generally to signify, first, a separate, independent origin, and, second, convergent evolution, leading to a like use and to a superficial similarity in structure. The trend of thought has been in that direction, even though a considerable number of biologists, agreeing with Boyden, have stated their belief that analogy should apply to any agreement in general function, whether or not the structures involved are homologous. But even those who accept this broader definition are wont to write such phrases as "analogous only" or "analogous but not homologous," to indicate that they too associate with the term analogy a connotation of independent origin. Dr. Boyden writes that when he took a poll of recent text-book opinion he found that a very large majority of the authors associated independent origin or superficial similarity with analogy. The "last word" (Webster's New International Dictionary of the English Langauge, second edition) gives the biological definition of analogy as "correspondence in function between organs or parts of different structure and origin;—distinguished from *homology*." This dictionary definition does not interpret all usage, but it seems to reflect the opinion of the majority of present-day biologists.

Analogy, like homology, should apply to both functions and structures. As Tait pointed out, analogy was originally a term applicable to structures. Many biologists, however, would treat it as essentially pertaining to functions. But structures and functions exist together as inseparable manifestations, as we noted in applying the homology concept to both. Since homology expresses the relation between characters, whether of function or structure, that are fundamentally alike and of common origin, the contrasting term, analogy, should apply to either functions or structures, when these are only superficially alike and are not monophyletic.

Ordinarily, in testing the phyletic significance of a character, the biologist will contrast homology and analogy. But when a broader antonym is needed, without restriction as to agreement in function or superficial similarity, the character involved may be denoted as nonhomologous (or as polyphyletic, polygenetic or heterophyletic). When the whole emphasis is on community of origin, such terms as monophyletic, monogenetic and homophylic are available. The term "analogous" is now properly applied, I think, only to structures and functions which serve the same use, but which are of independent origin and history. There seems to be no need for a return to an older concept of either analogy or homology.

SUMMARY

Boyden urges that we return to Owen's original, century-old definitions of homology and analogy—analogy to signify a similarity of structures in use, without regard to fundamental agreement in structure or evolution; that is, without regard to homology; and homology to indicate a basic agreement in structure and relative position, without regard to functional similitude.

But the concept of homology has evolved through the century, particularly under the influence of the doctrine of evolution. Homology has come to signify an agreement in evolutionary derivation and in embryonic development.

The traditional and persistent limitation of the homology concept to structures has overemphasized morphology and is inconsistent with the modern view that structures and functions are inseparably associated. It is desirable that the term homology be regarded as applicable also to intrinsic functional mechanisms, reflexes, behavior patterns and other functional attributes, when they indicate a common heritage.

Attempts to dissociate "serial homologies" from "true or special homologies," and various proposals to break down homology into a series of relations each with a separate name, have largely been abortive and are not regarded as wise. A consideration of homologies between diffuse elements helps to clarify the general picture. Endless inconsistencies would arise from the application of suggested restrictions of the homology concept.

Homologous relationships are very complex. There are many degrees of specificity in homology. Two characters may be homologous from one point of view but not so from another. Where to draw the line is a function of the special needs in any comparative study. Many complexities in homological relations come to mind when we review the facts of anatomy, variation, genetics and experimental embryology, and the uncertainties may be accentuated in studying closely related kinds of animals. Such irregularities encumber almost all biological concepts, but destroy neither their validity nor their usefulness.

What may be called independent homologies—more or less identical but independent modifications of homologous structures or functions, agreeing with typical homologies in all respects other than time of origin—provide a troublesome transition between homologies and analogies. There are genetic discontinuities of various kinds and degrees in the lineage of characters.

A modern concept of analogy is that of the agreement in use of characters (structures or functions), which have had a distinct evolutionary origin. There seems to be no special need for a return to a century-old concept of either analogy or homology.

Both concepts—of homology and of analogy—should be recognized as involving grave complexities. These ideas involve the same sort of inexactitude that is inherent in such principles as those expressed in Haeckel's biogenetic law and Dollo's law of irreversible evolution. Precision in any of these concepts should not be allowed to transcend the complexities that exist. Despite these difficulties, the concepts of homology and analogy retain, in their evolved, modern meaning, a place of importance and value in biology.

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DISTRIBUTION AND VARIATION IN POCKET GOPHERS, *THOMOMYS TALPOIDES,* IN THE STATE OF WASHINGTON

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INTRODUCTION

FROM an evolutionary standpoint the pocket gophers of the genus *Thomomys* comprise one of the most plastic groups of North American mammals. Their range of variation in morphological characters is extreme. In color they vary from nearly white in some desert species to almost black in others. In the skull, variations in ridging, size, proportion and in shape of the cranial bones, are clearly exhibited. The habits of pocket gophers are such that relatively minor topographic or environmental barriers often effectually limit their areal distribution, although the same barriers may have little or no effect on other vertebrates. These conditions have contributed to the formation of a large number of subspecies (geographic races) of pocket gophers in the western United States, each comprising a complex distinguishable by average differences in size, color or cranial characters from its kindred subspecies.

The present report is based on a study of the distribution of mammals in a region of which parts were recently subjected to continental glaciation and of which other parts were strongly affected by the near-by ice. We have attempted to point out the relationships between the present distribution of the pocket gophers of Washington and the probable history of their origin, migration and eventual geographic isolation. We have sought to interpret on a genetic basis, wherever possible, the variation that is now exhibited by these animals.

Our source materials include 710 specimens of gophers collected by us or examined in museums over the past ten years. Our largest series were taken from the prairies around the south end of Puget Sound, the Puget Sound Trough of geological terminology, in the three winters of 1938–1941. Topotypes of all races of pocket gophers found in Washington and the type specimens of several races were available to us. Body measurements and weights were made in the field by each of us, and cranial measurements were made by one of us (Dalquest) in the laboratory. Specimens used for demonstrating subspecific differences were fully adult but not "very old" animals. We did not have sufficiently large series of individuals of the same age and sex from single localities to compare populations by means of standard errors.

For the use of specimens in their care and valuable assistance in other ways, we are deeply indebted to Dr. H. H. T. Jackson, U. S. Fish and Wildlife Service, Mrs. Martha Flahaut, Washington State Museum, Dr. George E. Hudson, Charles R. Conner Museum, and Dr. E. Raymond Hall of the Museum of Vertebrate Zoology, of the University of California at Berkeley. From the last mentioned the writers acknowledge critical assistance in the preparation of this paper.

IMMIGRATIONAL HISTORY OF THE POCKET GOPHERS OF WASHINGTON

The pocket gophers of the state of Washington may be classed for convenience into two groups: a relic group, which occupied the state in preglacial or interglacial times, and a group of immigrants from the south and east which entered the state shortly after the Pleistocene. The earliest described race of the relic group is *douglasii,* and this group is therefore referred to as the *douglasii* group of subspecies. For a similar reason, the immigrants are termed the *fuscus* group.

It is difficult to select morphological characters which will consistently separate the two groups. Generally speaking, the gophers of the *douglasii* group are larger and possess larger, heavier skulls with relatively longer rostra and more flaring zygomatic arches. Exception must be made for certain races of the *douglasii* group found in the Puget Sound area which do not show all these differences.

The *douglasii* group appears to be more restricted in habitat than the *fuscus* group. The *douglasii* gophers are found in the grassy prairie lands of the Palouse country of southeastern Washington, in glacial outwash and river terrace prairies of western Washington, in the open, grassy prairies of the Columbia River Valley of southern Washington, and in the alpine meadows of the Cascade and Olympic mountains. They prefer well-watered,

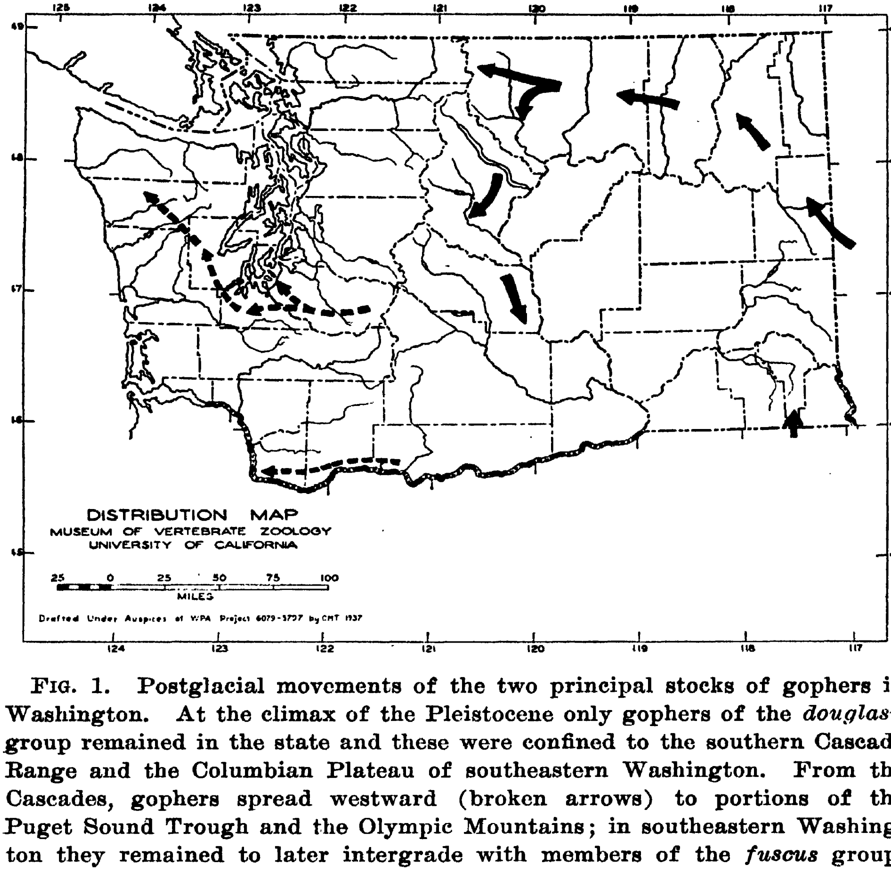

FIG. 1. Postglacial movements of the two principal stocks of gophers in Washington. At the climax of the Pleistocene only gophers of the *douglasii* group remained in the state and these were confined to the southern Cascade Range and the Columbian Plateau of southeastern Washington. From the Cascades, gophers spread westward (broken arrows) to portions of the Puget Sound Trough and the Olympic Mountains; in southeastern Washington they remained to later intergrade with members of the *fuscus* group. With the retreat of the glacial ice, gophers of the *fuscus* group invaded (solid arrows) from Idaho and northern Oregon.

grassy, prairie lands free of even moderately thick forest or brush. An exception is the desert-inhabiting race, *devexus*.

Gophers of the *fuscus* group, on the contrary, occur in many kinds of habitats. We have found them in baked, desert loess-clay, grasslands, ground moraine, open woods, alpine meadows, and damp, almost marshy lands.

With the exception of *Thomomys talpoides tacomensis*, taken on agricultural land, we have found the *douglasii* gophers only in relatively large colonies. Most of the colonies included from fifty to several thousand individuals living in close proximity to each other. Even near the main colonies, small areas of land capable of supporting from one to ten gophers almost always are unoccupied.

Gophers of the *fuscus* group may be abundant in, and occupy all of, a suitable area, but seem not to live as close to each other as do individuals of the *douglasii* group. It is almost the rule, in Washington at least, to find *fuscus* gophers in small groups. This is true even on extensive and uniform terrain which gophers might be expected to occupy *in toto*. The antisocial and independent habits of the *fuscus* gophers and their high degree of tolerance of variations in habitat probably account in part for their success in extending their range at the expense of the earlier established *douglasii* gophers.

Previous to the last Pleistocene glaciation (Wisconsin Glaciation in eastern Washington, Vashon Glaciation in western Washington), pocket gophers of the *douglasii* group apparently occupied all the potential range of the species in the state. This range might have included all of Washington from the Cascade Mountains eastward. The forested areas of western Washington probably never supported gophers.

The descent of the Vashon-Wisconsin ice sheet completely eliminated gophers north of the drift border, in general, the area north of the east-west segment of the Columbia River in northeastern Washington (Flint, 1937, p. 212). Frigid climate prevailing in the Cascade Mountains as far south as Mount Rainier is thought to have exterminated gophers north of this area. The withdrawal of the ice some ten thousand years ago, then, found the *douglasii* gophers restricted to the southern Cascade Mountains, the Columbian Plateau, and southeastern Washington.

The douglasii gophers isolated in the southern Cascade Moutains were extremely plastic, in a systematic sense. Within this area three geographic subspecies occur today: *Thomomys talpoides shawi,* in the Mount Rainier area; *immunis,* in the Mount Adams area; and *limosus,* in the Columbia River Valley. Individuals of the *limosus* stock migrated westward, early in Recent time, along the Columbia River, to certain Pleistocene river terraces in Clark County, where the race *douglasii* is now isolated.

The outwash train by which the *douglasii* gophers reached the Vashon outwash prairies in the Puget Sound area is now overgrown with forest. To the best of our knowledge no gophers now occur in this train. There is an isolated population of the race *yelmensis* at Vail, Thurston County, and a distinct race (*glacialis*) near Roy, Pierce County, north of the Nisqually River and north of the population on the prairie at Vail. Outwash prairies, free of gophers but possessing Mima mounds (unique structures formed by pocket gophers; Dalquest and Scheffer, 1942), connect the gophers at Roy with those of a similar but distinct race, *tacomensis,* found near Steilacoom, Pierce County.

Outwash prairies, some of which bear Mima mounds, connect the population at Vail with another population of the race *yelmensis* near Tenino, Thurston County. *T. t. tumuli* occurs in Thurston County north of the range of *yelmensis.* Near Olympia, Thurston County, another distinct race, *pugetensis,* is found. West of Tenino, near Rochester, Thurston County, is another isolated population of *yelmensis.*

Mima mounds west of Rochester, in the Chehalis River Valley near Satsop, indicate that gophers migrated along this route to reach the outwash prairies on the southeastern base of the Olympic Mountains where the race *couchi* is now isolated on prairies near Satsop, and Shelton, Mason County (see Fig. 2). Gophers from these prairies probably moved up into the alpine meadows of the Olympics, where the race *melanops* is now found.

The *douglasii* group of gophers probably once extended in a continuous or nearly continuous band from Mount Rainier around the southern end of Puget Sound to the Olympic Mountains, on the glacial outwash prairies. The prairies consist of a deep bed of coarse gravel underlying a thin bed of silt-gravel. The coarse gravel causes rapid drainage of rainfall. In summer the soil on the prairies dries out so thoroughly as to kill seedling trees before they become established, and this permits the prairies to exist. They are semidesert areas surrounded by dense forests.

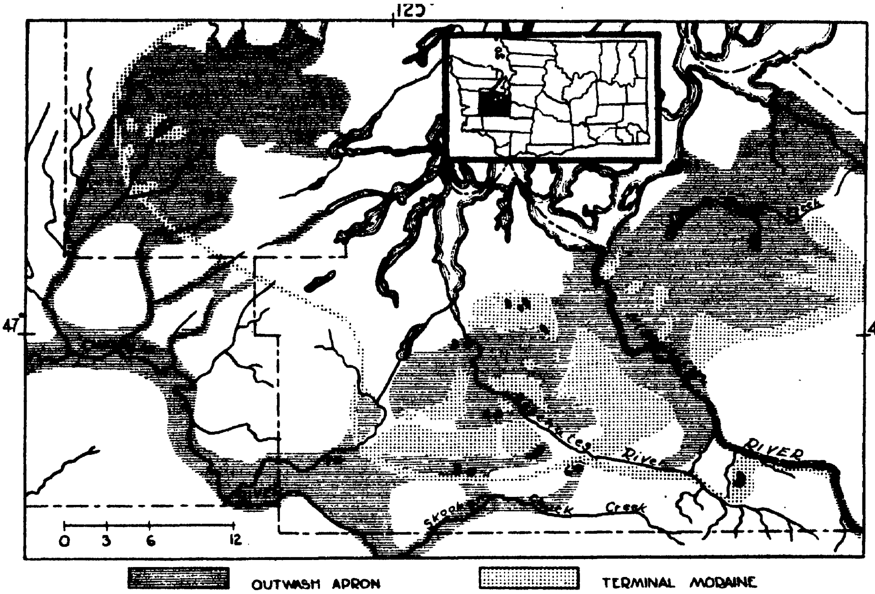

FIG. 2. Distribution of gophers in the Puget Sound area with relation to the Vashon outwash apron.

The *douglasii* pocket gophers seem unable to exist in forested areas, even on the outwash prairies. Only the subspecies *tacomensis* occurs on cultivated land, away from outwash prairie. With this exception, non-prairie areas or forested areas on the prairies serve as effective barriers to gophers. The once continuous band of outwash prairie extending around southern Puget Sound is now broken up by forests into numerous small prairies, resulting in the isolation responsible for the numerous subspecies of gophers in the Puget Sound area. Many former prairies which are now completely forested, bear remains of Mima mounds showing that gophers lived there in the past. At least one large prairie and two small ones, free of forest, possess Mima mounds, but no gophers now live there. The forest is invading all the prairies now supporting gophers; the area of some of these prairies has been reduced to less than a square mile. On Lost Lake Prairie, Mason County, we caught seven gophers, seemingly the entire population. The gophers of the Puget Sound area are doomed to extinction, perhaps within a century.

On the Columbian Plateau of central-eastern Washington there is a subspecies (*devexus*) of the *douglasii* group that was possibly distinct from the remainder of the *douglasii* group early in post-Pleistocene times. It is a small, pale race, seemingly well adapted to the desert region it occupies. This race has the flaring, angular zygomatic arches of the *douglasii* group, and intergrades evenly with *limosus* and *columbianus*, kindred members of the group. Intergrades between *devexus* and members of the *fuscus* group, on the other hand, show dominance of the color factors of one subspecies or the other in that heterozygous individuals have the color of one race or the other rather than being intermediate in color. Some intergrades between *devexus* and members of the *fuscus* group show the color of both parent races on the body of one individual. This condition, seemingly a case of reversal of dominance caused by environmental conditions at the time of moult, is discussed in detail later.

Although *devexus* belongs to the *douglasii* group, it is much different in skull and color from other members of that group. Therefore, and because it has an extensive geographic range, *devexus* is judged to have been isolated from other members of the group for a considerable time. The Columbia River on the north and west and the absence of desert conditions to the north, east and west doubtless confined it in these directions. A barrier does not exist to the south of the range of *devexus* at the present time. The past existence of a barrier to desert forms is indicated not only by the restricted range of *devexus* but by the close relationship of a number of mammals in southeastern Washington to those of the Simcoe Mountain Range of the southern Cascades. The barrier referred to, we have named the Simcoe Bridge. It is conceived of as consisting of the Simcoe Anticline, a high ridge which reaches from the southern Cascades to the Columbia River Water Gap, near Wallula, and this bridge continues on east of there, in the Bunchgrass Hills. A century ago this bridge was an area of bunch-grass, but most of the grass has since been supplanted, largely by sagebrush. When the Wisconsin ice was at its maximum extent, the Simcoe Bridge presumably had a cooler and more humid climate than now. This climate allowed dark-colored, *limosus*-like pocket gophers of the *douglasii* group to live in a grassy area, somewhat resembling an alpine meadow, that stretched from the Cascades to southeastern Washington. Many of the tributaries of the Columbia River lie to the north of the border of the Wisconsin drift. These probably held little or no water while the ice sheet was in place. Therefore the volume of water in the Columbia may have been much less than now and the river less of a barrier to mammals. The Columbia has frozen over in historic times, and the black-tailed jack rabbit is known to have extended its range in Washington by crossing on the ice (Couch, 1927). Presumably the river froze over more regularly in Wisconsin and early Recent times, and pocket gophers might have crossed the river through burrows in snow covering the ice (see Davis, 1939, p. 240).

Increasing aridity, following the retreat of the Wisconsin ice, closed the Simcoe Bridge to the dark-colored gophers. This same aridity, in conjunction with a cover of sandy, glacial outwash allowed the pale *devexus,* hitherto confined to the Columbian Plateau, to extend its range southward along the Columbia River Valley. The area occupied was only the narrow, desert-like valley of the Columbia itself. The excessive grayness of the gophers found near the Columbia River in Walla Walla, Benton and Yakima counties may represent the influence of this minor movement.

The race *columbianus,* from Walla Walla County, is essentially a population of intergrades between *devexus* and *aequalidens,* but with certain distinctive features of color, size and skull.

The withdrawal of the Wisconsin ice from northeastern Washington freed the land north of the terminal moraine for occupation by gophers. Gophers invaded the area from the east. These gophers exhibit no characters different enough from those of the race *fuscus* to warrant recognition of them as a separate race. Apparently the ground moraine and glacial drift topography exposed by the withdrawal of the ice was so homogeneous that no differentiation took place in the westward migration of the gophers across northern Washington. The race *fuscus* moved southward along the Cascades until it crossed the Wenatchee Mountains and occupied the Yakima Valley to the mouth of the Yakima River.

Another race (*wallowa*) of the *fuscus* group moved northward in the Blue Mountains of northeastern Oregon into the Blue Mountains of extreme southeastern Washington, where it intergraded with *aequalidens,* of the *douglasii* group. The gophers of the higher parts of the Blue Mountains are actually intergrades between *wallowa* and the *douglasii* gophers to the north, but are referable to *wallowa* (see systematic account). These immigrations of *fuscus* gophers almost completely surrounded the *douglasii* gophers on the Columbian Plateau of southeastern Washington (Fig. 1).

HABITS OF POCKET GOPHERS WITH RELATION TO SPECIATION

The general habits of pocket gophers have been described in detail by many authors (Bailey, 1915; Scheffer, 1931). We should like to call attention, however, to certain habits that have played an outstanding role in the evolution of the subspecies studied by us. (1) Pocket gophers are almost completely fossorial, rarely appearing on the surface of the ground. (2) They seem to be solitary and, although tending to live in communities, have no social organization; intermingling of the sexes takes place only during the breeding season (Scheffer, 1931). (3) They live in meadows or grasslands; forest or brush serves as an effective barrier to their movements. (4) They eat or otherwise destroy the roots, stems and leaves of plants; but we judge that, in the majority of cases, the burrowing and mounding habits of gophers stimulate plant growth, by loosening the soil, to a degree that compensates for the destruction of vegetation within the home territory of any individual (Dalquest and Scheffer, 1942). This natural balance allows a suitable habitat to be indefinitely occupied by gophers without depletion of the food supply, provided, of course, that disruptive changes in the environment are not created by outside forces. (5) Gophers tend to remain within a relatively small territory throughout their life.

Climatic, topographic and edaphic conditions in the state of Washington are such that habitats suitable for gophers occur as numerous small "islands" surrounded by uninhabitable territory. The total population of gophers within the range of any described race may number many thousands. The range of a race is not continuous but is made up of countless independent "sub-populations" including tens, hundreds or thousands of animals.

The effect of this isolation of individual units within a larger taxonomic group is pronounced. Mutations appearing in a small, isolated population may be lost, may be retained in a certain proportion of the population or may become fixed and probably homozygous for the entire population, in some populations seemingly without the operation of natural selection. The smaller the population, the more rapidly a factor becomes lost or fixed (Dobzhansky, 1937, p. 182). A race of pocket gopher, then, may be regarded as a group of populations, in each of which the trend of variation is along independent lines. For example, if one were to arrange graphically on a distribution curve the measurements of a single bone in all members of a subspecies of gopher, the curve would exhibit minor nodes, corresponding to the sub-populations, along its length.

The geographic races of pocket gophers in Washington are isolated from each other by topographic and ecologic barriers, such as rivers and mountain ranges, which are of a relatively stable and permanent nature. The barriers isolating sub-populations within a race, forests, for example, are temporary and, although they may stand for years or even centuries, they can be expected eventually to break down and permit intermingling of sub-populations.

Microgeographic races within the range of a subspecies are familiar to all students of *Thomomys*. For the most part these morphologically differentiated populations are separated only by average differences that may represent minor mutations in the multiple factor series for size or color. A striking mutation in a population from Glacier Basin, Mount Rainier National Park, is shown by three or four specimens which represent two generations. They have an extra cranial bone, a small "internasal," situated between the nasals and the frontals (Fig. 3). Probably the bone has no selective value, and may even be a hindrance to the individual which possesses it. The factor or factors for this bone seem to be fluctuating by chance in a small population, and may later become fixed or lost.

The independent evolution of isolated populations within the range of a subspecies and the subsequent intermingling of these populations through the removal of temporary natural barriers, represent diametrically opposed processes. The first tends to establish relatively homozygous entities, whereas the second tends to destroy them.

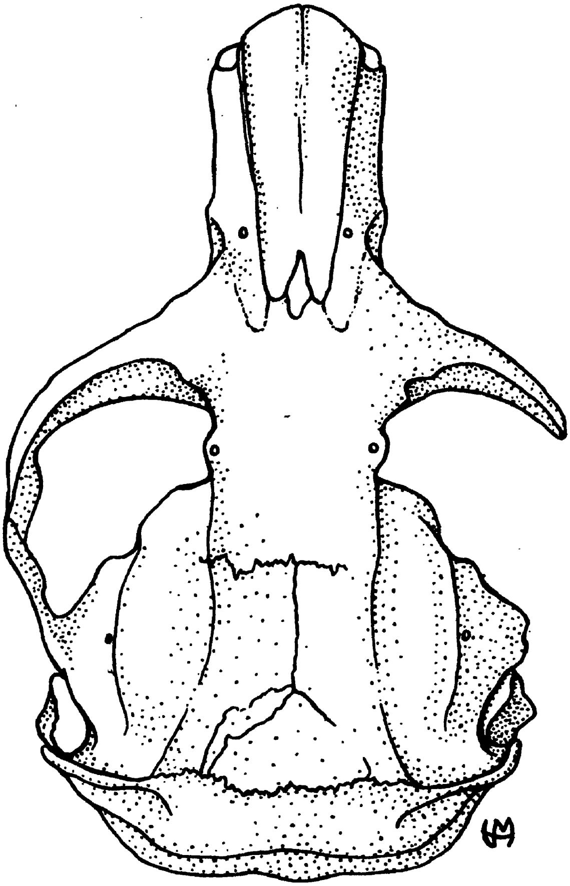

FIG. 3. A cranial mutation in *Thomomys talpoides shawi.* Three of four specimens from an isolated glacial circue on Mount Rainier, Pierce County, possess this "internasal bone." The bone is present in at least two different generations. 3 × natural size.

Evolution of the geographic race as a whole may be influenced in two ways as a result of these processes. The mingling of a population relatively homozygous for a mutation with a population lacking the same mutation might result in the gene again fluctuating in frequency in each generation in the combined populations. The gene might thereby eventually become either lost or fixed. A mutation might, through a series of "conquests," be spread throughout the geographic race, and with each conquest its chances of ultimate survival would be increased. Such a hypothesis accounts for the differences between the numerous geographic races of pocket gophers, as well as for the countless differentiated populations of less than subspecific rank.

Secondly, microgeographic isolation of small populations would provide reservoirs of differences upon which natural selection might act. A mutation of slight selective value is likely to be lost in a large population, on the basis of chance alone. But if the mutation is homozygous throughout a small population, which mingles with other populations at a later date, its chances for survival might be markedly increased because of its selective value. Microgeographic races might also give a population of gophers an added advantage in meeting such changing environmental conditions as followed the retreat of the continental glaciers from the state of Washington.

Broadly speaking, the differences separating any population of gophers from surrounding populations might have been derived in at least two ways: (1) from mutations which became homozygous for the whole population or which are still fluctuating, that is, which are phenotypically expressed in a certain proportion of the population; (2) by the loss of certain allelomorphs in an isolated population derived from a population in which certain factors were fluctuating, while in the other, original, population these factors might have become fixed. Nearly all microgeographic variations represent slight average differences in size or proportion of body, color of pelage or size or proportion of cranial bones. We feel that most differences are the result of slight changes in multiple factor series. Some changes in cranial bones may represent single factor mutations.

Size and cranial aberrations or anomalies of a quantitative nature, resulting from genetic changes, are difficult to separate from non-genetic variants of the usual modification curve. One cranial aberration, that of the "internasal" bone, has already been discussed.

Quantitative aberrations in color are more easily detected. A number of these have been found in gophers in Washington. The most striking is the absence of the proximal color band of the fur. "Recessive spotting" is the commonest type of color aberration found by us. Gophers with recessive spotting are flecked dorsally or ventrally with small, irregular, white spots. The spots may vary in number from one to a dozen on an animal and are largest and most numerous on the ventral surface.

One gopher from Mount Adams, Klickitat County, is blotched with white on the ventral side and possesses a white line on the head, extending from the nose, posteriorly between the eyes to the forehead. Whether this specimen represents an extreme case of recessive spotting or involves another type of mutation can not be determined.

PROBLEMS OF VARIATION IN RACES OF POCKET GOPHERS FROM THE PUGET SOUND AREA

Although the entire state of Washington is included within the scope of our investigation we have studied with the greatest intensity the variation among gophers of the prairies of the Puget Sound area. Here six races are concentrated in a relatively small area where the environmental factors that might have contributed to their speciation are more plainly evident than in the parts of eastern Washington which are occupied by gophers.

In 1899 Merriam named *Thomomys douglasi yelmensis,* the first subspecies of gopher to be recognized from the Puget Sound area. Twenty years later Taylor (1919) named a second subspecies, *tacomensis,* from a locality thirty-five miles northwest of the type locality of *yelmensis.* At that time he remarked: "The pocket gophers of the isolated prairies of western Washington show the effects of segregation. Broadly speaking, one may say that those inhabiting each prairie represent a local variant. While the characterization of each of these would be confusing, the recognition of the more obvious forms is desirable. *Thomomys douglasii douglasii* is one of these, *T. d. yelmensis* another, and *T. d. tacomensis* a third." Although the differences separating the isolated populations of gophers in the Puget Sound area were recognized at that time, it was not until twenty years later that the subject was reexamined by Goldman (1939) and Dalquest and Scheffer (1942).

Certain factors appear to have been more significant than others in the evolution of the gophers of the Puget Sound area. The time element, or period of isolation, is relatively short and is thought to have been of approximately the same duration for all of the described races. As previously stated, the ancestors of the Puget Sound gophers moved down the narrow Nisqually Valley from Mount Rainier as a homogeneous stock. We conceive of this migration as the cumulative seasonal progression westward of young gophers toward the attractive but unoccupied area, rather than as the pioneering advances over long distances by adult animals. The actual advance of any one gopher in its lifetime may have been but a few hundred feet. After the formation of the Vashon Puget outwash aprons, ten to twenty thousand years ago, additional time was required for the development there of vegetation capable of sustaining gophers, and then for the invasion of the aprons by gophers. About ten thousand years would represent the maximum length of time that any population of Puget Sound gophers has been isolated.

Mineralogically, the rock materials composing the

Puget Sound prairies are alike. All were formed of glacial drift reworked and redeposited by water.

The prairies occupied by gophers lie at nearly the same distance above sea level, between tidewater and an elevation of 500 feet.

Records of the United States Weather Bureau show that the yearly variations in temperature and precipitation on any prairie exceed the variations among the different prairies in any one year, and as a consequence the climate may be considered uniform over all the prairies.

Although the individual prairies are identical in the above-named ecologic features, they do exhibit striking differences in depth of soil, size of soil particles and vegetative cover—all closely related attributes. Outwash prairies consist of a deep layer of coarsely stratified yellow gravel of unknown thickness containing little interstitial sand or silt and a layer of topsoil of black silt-gravel. We suppose that the outwash aprons originally consisted of a layer of stratified gravel covered with a layer of flood-plain silt. The activities of plants and animals, especially of moles (*Scapanus*) and pocket gophers, have thoroughly mixed a part of the stratified gravel with the silt, forming the topsoil. The quantity of gravel mixed into the layer of silt determines the stoniness of the soil on the prairies. Where the original layer of silt was deep, as on Bush Prairie (in this case more than five feet), the ordinary burrowing activities of animals did not extend down to the surface of the gravel and, as a consequence, the soil there is almost pure silt. On Scotts Prairie the layer of silt was, originally, only a few inches thick, and the present soil is extremely stony. On every prairie in the vicinity of Puget Sound the stoniness of the soil is inversely correlated with the depth of the soil.

On all but the deep-soiled Bush and Roy prairies, pocket gophers have accumulated great masses of soil, known as Mima mounds. The complicated formation of these mounds has been discussed in detail by Dalquest and Scheffer, *loc. cit.* Mima mounds resemble great spheres, partially buried in the earth. On many prairies these mounds are now the only places occupied by gophers.

Differences in vegetation on the prairies inhabited by gophers are difficult to measure at the present time. Grazing by sheep and cattle and the introduction of weed plants have radically changed the composition of the vegetation on most of the prairies, so that any qualitative differences in vegetation which once might have existed among them can no longer be seen. Considering the nearness of the prairies to each other and the similarity of many of the environmental factors, it is likely that any original qualitative differences in vegetative cover were slight. Quantitatively there are noteworthy differences; the deep-soiled prairies bear a lush vegetation of grasses and annuals, whereas the thin-soiled prairies bear a sparse cover consisting mainly of mosses and lichens.

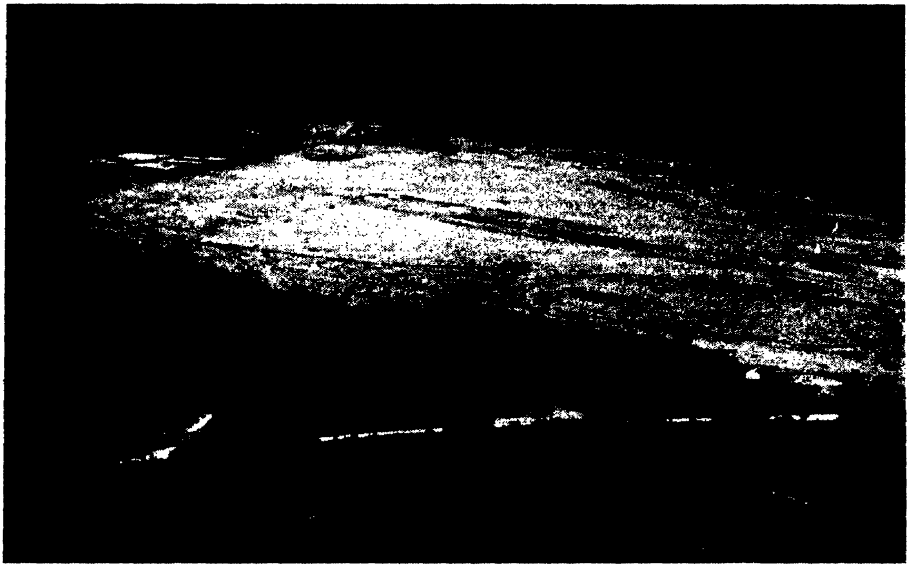

FIG. 4. A prairie inhabited by gophers in the Puget Sound area. Scotts Prairie in Mason County is one of the native grasslands that dot the timbered coastal region. These consist of deep beds of coarse gravel covered by soil layers of porous silt or silt-gravel. The soil layers become too dry in midsummer to support the growth of seedling trees. Scotts Prairie is the type locality of *Thomomys talpoides couchi.*

Three important, measurable differences in these prairies, namely, depth of soil, size of stones or smaller inclusions in the soil and vegetation, thus result from a single factor—the difference in the depth of the layer of soil. If any or all of these differences has acted as a selective factor in the evolution of the gophers, variation in the populations should be correlated with depth of soil on the prairies. In an effort to determine this we have collected series of study specimens of pocket gophers and for each prairie have recorded the edaphic and vegetative conditions.

DESCRIPTION OF THE PRAIRIES INHABITED BY GOPHERS IN THE PUGET SOUND AREA

The following brief descriptions of the Puget Sound gopher prairies are arranged (with the exception of that of the Steilacoom Delta) in order of decreasing depth of soil, or, in the case of prairies which have Mima mounds, in order of decreasing height of the mounds.

1. *Bush Prairie,* 4 mi. S Olympia, Thurston County (type locality of *pugetensis*), includes the Olympia airport and fields to the west of the airport. The soil here is more than 5 feet deep, soft and free of pebbles; no Mima mounds are present; vegetation is high and rich on areas ungrazed by cattle.

2. *Roy Prairie,* 2 mi. S Roy, Pierce County (type locality of *glacialis*), has an area of deep soil, about 4 feet thick, where gophers occur, just below and south of a Pleistocene terrace on the north border of the prairie. The soil resembles that of Bush Prairie, but is shallower and has a few pebbles. Vegetation is high and lush. One mile south of the deep-soiled area the soil becomes thin and the prairie is studded with kettles and Ford mounds. A few Mima mounds occur at the northern edge of the shallow-soiled area, and less than a dozen old gopher workings were discovered there.

3. *Rocky Prairie,* 5 mi. N Tenino, Thurston County (type locality of *tumuli*), is extensive and has the largest

Mima mounds now inhabited by pocket gophers in the Puget Sound area. The soil is stony, but in some places 4 feet deep. Vegetation on the mounds is dense, but it is scant or absent in the areas between the mounds.

4. *Rochester Prairie,* 2 mi. N Rochester, Thurston County (in range of *yelmensis*), has become separated from Grand Mound Prairie in relatively recent times. The Mima mounds are smaller than those on Rocky Prairie. The soil is stonier than that of Rocky Prairie, but the vegetation of the mounds is as dense, although where the gophers live the soil averages only about 3 feet deep.

5. *Grand Mound Prairie,* 2 mi. S Tenino, Thurston County (type locality of *yelmensis*), closely resembles Rochester Prairie, but the Mima mounds are slightly smaller. The stony soil, of about the same depth, and the amount of vegetation on the Mima mounds of these two prairies seem alike.

6. *Vail Prairie,* 1 mi. W Vail, Thurston County (in range of *yelmensis*), has soil rather shallow, averaging 3 feet or less in depth where the gophers live, and stonier than that of Grand Mound Prairie. No uncultivated or ungrazed land remains on the prairie, and its vegetative cover now is not comparable with that of other prairies. The remains of Mima mounds, nearly eradicated by cultivation, are smaller in diameter than the mounds of Grand Mound Prairie.

7. *Lost Lake Prairie,* 15 mi. NNE Satsop, Mason County (in range of *couchi*), has been nearly eliminated by forest. The soil is thin, not more than one foot deep, and rocky; the vegetation is sparse. Mima mounds are low and poorly developed. Less than a dozen gophers are thought to exist here.

8. *Scotts Prairie,* 4 mi. N Shelton, Mason County (type locality of *couchi*), is rather small (Fig. 3). The soil is only about 9 inches thick and is stony; the vegetation is scant. Mima mounds here are the smallest known to us, being less than 2 feet high.

9. *The Steilacoom Delta,* 2 mi. NW Steilacoom, Pierce County (possibly the type locality of *tacomensis;* certainly within a few miles of the type locality). Here pocket gophers occur on the topset beds of a great delta built into the Pleistocene Lake Russell (Bretz, 1913, p. 137). The soil layer here lacks the distinct vertical stratification typical of the outwash prairies. Gophers are almost absent from adjacent outwash prairies and are now restricted to non-prairie agricultural lands on the delta where the soil is reddish sandy-gravel. Pocket gophers could not have lived in the timber of the delta before it was cleared for agriculture. They must have lived on some of the outwash prairies to the eastward and later invaded the delta. A few gopher workings and some low Mima mounds were found on prairies which grade gradually into the red-soiled topset beds of the delta.

VARIATIONS IN SIZE OF GOPHERS FROM THE PUGET SOUND AREA

Five races of gophers, living on eight separated prairies in the Puget Sound Trough, may be divided into three size groups: (1) In the group of largest size, three races are included. Two are from the deep-soiled prairies (*glacialis* and *pugetensis*) and the other from Rocky Prairie (*tumuli*) where the Mima mounds are large. (2) On the three prairies where the Mima mounds are of medium size, the gophers (*yelmensis*) are also of medium size. (3) The smallest race of gopher found in the Puget Sound area (*couchi*) lives on Lost Lake Prairie and Scotts Prairie, where the soil is thinnest.

A sixth race of gopher (*tacomensis*) from the Puget Sound area lives in a habitat different from that of the other five. The soil conditions in its habitat are not comparable to those on the outwash prairies, where the lower limit of the soil layer is fixed by a "floor," or layer of stratified gravel. The habitat suitable for gophers includes only the soil layer above this floor. The sixth race lives in the reddish, sandy-gravel that constitutes the soil of the Steilacoom Delta. This delta lacks the restricting floor of pure gravel, and the vertical limits of the activities of gophers are regulated only by the whims of the individual. Thus, whereas the maximum depth of gopher habitat on the outwash prairies can be judged with accuracy, no accurate prediction can be made for the gophers living on the Steilacoom Delta. About all that can be said is that gophers would be expected to be of large size, as they are.

TABLE I

Correlation of Depth of Soil (or Height of Mima Mounds) with Size of Adult Male Pocket Gophers in the Puget Sound Area

Name of prairie	Specimens	Soil depth*	Total length	Weight
		ft.	*mm.*	*gm.*
Bush	14	5	223	123
Roy	20	4	225	128
Rocky	11	4	225	140
Rochester	16	3	215	117
Grand Mound	21	3	213	121
Vail	12	3	216	126
Lost Lake**	..	1	...	...
Scotts	13	¾	196	87

* Generalized depth where pocket gophers are living most abundantly.

** Only female gophers taken on Lost Lake Prairie. For comparison see Table III.

It is concluded that the size of the pocket gophers of the outwash prairies is positively correlated with depth of soil. This agrees with the conclusion arrived at by Davis (1938).

Having shown that size of pocket gophers is directly correlated with depth of the silt-gravel layer on the outwash prairies occupied and having presented evidence that populations about Puget Sound originated from a common stock and therefore had identical or nearly identical gene compliments, we deduce that depth of soil, or some function therefore, has acted as a selective factor to limit the size of the gophers.

As to selection, there are two possible methods by which it might have been brought into play. In each population, new factors for size might have appeared. The size most favorable for the depth of soil of the habitat occupied may have been retained through selection. Serious objections to this view are: (1) the small size of the populations (larger in the past, it is true, but still small as compared to other species of rodents), which would tend to limit the appearance of new factors; and (2) the relatively short period of isolation (less than ten thousand generations), which we feel would scarcely allow for the origin and spread of the necessarily large number of mutations and the subsequent elimination of all but the most favorable. It seems improbable that each of the six races had a favorable mutation soon after it was isolated.

We are inclined to a second view, namely, that in the original population occupying the outwash aprons, size was variable and was controlled by a number of pairs of alleles in a multiple factor series. Under isolation and the restricted environment of the silt-gravel layers on the prairies, individuals with factors for a size most efficient for their particular environment were favored by selection, until the entire population became relatively homozygous.

There is thus no necessity for assuming that new factors for size appeared, but only that there was a loss of one or more alleles and that there occurred a fixation of factors already present. Newly acquired factors may, it is true, have contributed to the end result. Hagedoorn and Hagedoorn (1921) show that the smaller a population (and ours are small), the more rapidly a factor becomes fixed or lost, owing entirely to the operation of the laws of chance.

In addition to absolute size of body and skull, the relative size of parts should be mentioned. In general there is a strong, positive correlation between size of body and size of skull. In specimens of *yelmensis* examined the correlation between condylobasal length and total length of body had a Piersonian coefficient of 0.61. In *pugetensis* the coefficient of correlation between body length and weight was found to be .68. The relative sizes of the various parts of the skull vary considerably between races and are generally reflected in the standard measurements taken. A slightly larger body in one race than in another is accompanied by a much larger skull and on the larger skull, in response to larger muscles, there are strong ridges, crests and tuberosities which are only faintly indicated or absent on the skulls of races with smaller bodies.

The foregoing quantitative characters are all expressions of size and are phenotypic expressions of the genes controlling size. Sumner (1930) found size in *Peromyscus* to be explained best by the multiple factor hypothesis and this hypothesis probably applies also to the pocket gophers.

VARIATIONS IN COLOR OF GOPHERS IN THE PUGET SOUND AREA

All prairies inhabited by pocket gophers in the Puget Sound area lie within the Humid Transition Life-zone. Subspecies of birds and mammals from within this life-zone are, with few exceptions, darker or more "saturated" than subspecies from inland areas to the east. This is true of pocket gophers in Oregon and California, but not in the Puget Sound area. Subspecies of gophers around Puget Sound vary considerably in color, but all are lighter than some of the darker subspecies from east of the Cascade Mountains, although some races from the latter region are lighter than those of the Puget Sound area. It should be noted here that one post-Pleistocene emigrant race of the *douglasii* group, *aequalidens,* in southeastern Washington retains its dark color, although surrounded by pale races.

No correlation was found between the color of pocket gophers from the various prairies around Puget Sound and any observable factor in their environments. Certainly color is not correlated with depth of soil. This lack of correlation in color of gophers on the outwash prairies, where differences in habitats are easily observed, leads us to think that there is no strong selective factor for color operating on the races of the Puget Sound area. In these same populations, where depth of soil has acted to determine the mean size of the pocket gophers, color factors seem to have become lost or fixed irrespective of any discernible selective factors. It seems improbable that the gophers of the Puget Sound area have been immune to the influence which operates in the humid coastal area to produce dark color in most vertebrates. We conclude that depth of soil, in a relatively short time of isolation, is a much more powerful selective factor for size than is any discernible selective factor for color. Probably factors, of the environment, selective for color are present, but their effect is so slight as not to overcome the fixation resulting from chance combinations of alleles of a multiple factor series. If different alleles have become lost or completely fixed on each prairie, this would account for the variations in color from prairie to prairie and the almost complete lack of overlapping of color in the several races.

QUALITATIVE DIFFERENCES IN GOPHERS OF THE PUGET SOUND AREA

Two examples of variation of a qualitative nature have come to our attention. One, the presence of an extra cranial bone, the "internasal," has previously been discussed (p. 318). This bone was found in one old adult and two younger animals, suggesting that a spontaneous mutation arose and persisted over at least two generations. A character of no selective value arising in such a way in a population of gophers might, in a few hundred generations, become homozygous for the entire population. We think that the internasal bone and at least some of the lesser cranial characters such as processes, prominences and angularities found among gophers are single factor characters and as such are fluctuating more rapidly than multiple factor characters. Sumner (1934, p. 145) emphasizes the fact that in the deer mouse, *Peromyscus*, specific differences studied by him have all been multiple factor characters. Qualitative morphological characters, such as the processes, prominences and angularities typical of the skulls of gophers, however, are rare in *Peromyscus.*

Mutations present in only one or two isolated populations cannot be tested for correlation with environmental factors. Some such characters doubtless have selective value, positive or negative. Others, such as the shape of individual bones and position of auditory tubes, can be assumed to have little or no selective value.

A second variation, physiological rather than morphological, was observed in the tolerance of *Thomomys t. tacomensis* for a wide variety of habitats, including sandy-gravelly soil and thicket-covered land, in contrast to the behavior of the other five races of gophers in the Puget Sound area. We have emphasized throughout this report the complete restriction of the gophers of the Puget Sound area, with the exception of the one race, *tacomensis,* to the silt-gravel layer of soil on the outwash prairies and their absence from forested land. Also, each subspecies has rather distinct limits for size of the individual animal as shown by the small coefficients of variability. Nevertheless *Thomomys t. tacomensis* is an exception to the general rule, possibly because this race moved into soils lacking the definite horizontal limits of the silt-gravel layers on the outwash prairies before the modifying genes of the multiple factor series controlling variations in size were lost through natural selection. That the one race retaining a wide range of variability in morphological characters also retains a wide range of tolerance to environmental conditions, a range wide enough to permit it to invade land recently cleared by man, seems to be more than coincidental. Greater variability in size would scarcely account for greater variability in tolerance. We do not maintain that tolerance is, in this case, linked with size, or even that it is inherited in Mendelian fashion. We merely suggest the possibility of Mendelian behavior. It might well be that an original wide range in tolerance present in the gophers directly ancestral to the present races of the Puget Sound area has been lost to gophers that, for thousands of generations, have lived in the restricted silt-gravel layer of the outwash prairies. A series of genetic factors for range in tolerance might, in small, isolated populations, be reduced to the few factors of selective value necessary for existence in the homogeneous prairie habitat.

The race *tacomensis,* inhabiting a less stable environment than the other Puget Sound gophers, may have retained more modifying factors of the original size-regulating series. The same may be true of a series of multiple factors controlling tolerance. The two need not be linked, but may have responded to the same selective factors.

(*To be continued*)

MATING TYPES IN PARAMECIUM CAUDATUM

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Introduction

Studies of the sex of Protozoa have been undertaken only in recent years. Contributions to this problem are as yet few, of which the majority deals with various species of *Paramecium.*

It was Sonneborn (1937) who first discovered the two mating types in *P. aurelia.* He considered that the macronucleus rather than the micronucleus is differentiated as to sex. Kimball (1937) studied the inheritance of sex in *P. aurelia* and confirmed the results of Sonneborn, *i.e.,* the sex is determined by the macronucleus. Jennings (1938) investigated *P. bursaria* and found nine mating types falling into two independent groups. Tartar and Chen (1940) studied *P. bursaria* and concluded that it is the cytoplasm which is related to sex.

The mating types of *P. caudatum* have been studied by Giese and Arkoosh (1939) and Gilman (1940). The latter author found from nature five noninterbreeding groups of animals, each with two mating types.

The present work was started in May, 1942, using as material *P. caudatum* of Yunnan, China. Some interesting facts, which have not been recorded by the previous workers, have been observed. These are described in the present paper.

Materials and Method

Three lots of *P. caudatum* were collected from different localities: one (MA) from a small lake in Kunming, the second (MB) from a small pond in Sung-Ming about 50 kilometers from Kunming, and the third (MC) from a rice field in Cheng-Kung about 35 kilometers from Kunming. From MA 15 clones (C1–C15), from MB also 15 clones (C16–C30) and from MC 11 clones (C31–C41) were raised. Other clones (1*a*1, etc.) were raised from the exconjugants of the above clones. All the clones were cultivated in infusion of rice stalks in small finger bowls. The range of room temperature was from 12° C–24° C.

The clones were examined once in a few days in order to see if any endomixis occurred. This examination was made under a compound microscope. The stains used were acetocarmine and methyl green.

Tests for mating types were made as follows: Individuals from two different clones were mixed on a depression slide in a moist chamber. The mixture was examined frequently. If conjugating pairs occurred, these two clones were said to be of different mating types. The time from mixing of two clones to the appearance of conjugating pairs varied with various clones. Some conjugated immediately, while others required two days or more. In order to facilitate the mating reaction, the moist chambers containing the clone mixtures were placed in a dark chamber and were taken out only during examination.

Total-mount slides were made by fixing the animals in hot (60° C) Schaudinn's fluid and staining with iron alum hematoxylin or Feulgen's stain.

OBSERVATION OF MATING TYPES

This observation was continued for three months. The forty-one clones (C1–C41) collected from the field may be divided, according to their sex behavior, into three groups (groups 1, 2 and 3; Table II), each comprising two mating types (types I, II, III, IV, V and VI; Table II). No member of one group can react sexually with any member of the other groups. The three groups are thus independent of one another.

Clones from the exconjugants between type I and type II: Sonneborn (1937) discovered in *P. aurelia* that the descendants of the exconjugant may be all of the same sex as the progenitor, or of the opposite sex, or one half of them are of the same sex and the other half of the opposite sex to their progenitor.

To determine the types of descendants from exconjugants, the method employed by previous workers was followed. A single individual of one type was placed with a single individual of the opposite type on a depression slide. After conjugation, the four descendants of the two exconjugants (each of which had divided into two) were cultivated separately and resulted in four clones. The mating type of each of the four new clones was determined by examining its reaction against the two parental types.

The nomenclature used for the exconjugant lines in this investigation is that proposed by Jennings (1938). "To each pair was given a number, and the two members of a pair were called *a* and *b*. From each member two lines of descendants, derived from the first division of the exconjugant, were isolated; these were designated 1 and 2." Thus the pair 8 furnishes the four lines of descendants 8*a*1, 8*a*2, 8*b*1 and 8*b*2.

In most of my experiments, the behavior of clones derived from the descendants of exconjugants agreed with what Sonneborn found. However, some of the experiments on mating type I by type II gave different results. Among the 78 pairs of type I and type II, 75 pairs produced descendants either of type I or of type II, while the remaining three pairs (1st, 18th and 28th) produced descendants which were neither of type I nor of type II.

From these three conjugating pairs, 12 clones could be raised. But unfortunately some of them died and only 7 clones were raised. These surviving clones were 1*a*1, 1*a*2, 1*b*1, 1*b*2, 18*a*1, 18*a*2 and 28*a*1. The reactions of these seven clones against the two parental types and among themselves are shown in Table I, in which + indicates the occurrence of pairing while — indicates that no pairing occurs.

These seven clones were also tested against the four other types in groups 2 and 3. The results were all negative. Thus we may conclude that a fourth indepen-

TABLE I

THE MATING BEHAVIOR OF SEVEN EXTRAORDINARY CLONES RAISED FROM EXCONJUGANTS OF TYPE I BY TYPE II

	I	II	1*a*1	1*a*2	1*b*1	1*b*2	18*a*1	18*a*2	28*a*1
I	−	+	−	−	−	−	−	−	−
II	+	−	−	−	−	−	−	−	−
1*a*1	−	−	−	−	+	+	−	−	−
1*a*2	−	−	−	−	+	+	−	−	−
1*b*1	−	−	+	+	−	−	+	+	+
1*b*2	−	−	+	+	−	−	+	+	+
18*a*1	−	−	−	−	+	+	−	−	−
18*a*2	−	−	−	−	+	+	−	−	−
28*a*1	−	−	−	−	+	+	−	−	−

dent group, also with two opposite mating types has been derived by conjugation between the animals of type I and type II. Thus there are altogether 8 mating types falling into four noninterbreeding groups as shown in Table II.

TABLE II

THE MATING BEHAVIOR OF FOUR INDEPENDENT GROUPS

Source	Group	Type	1		2		3		4	
			I	II	III	IV	V	VI	VII	VIII
From nature	1	I	−	+	−	−	−	−	−	−
		II	+	−	−	−	−	−	−	−
	2	III	−	−	−	+	−	−	−	−
		IV	−	−	+	−	−	−	−	−
	3	V	−	−	−	−	−	+	−	−
		VI	−	−	−	−	+	−	−	−
Artificially raised in laboratory	4	VII	−	−	−	−	−	−	−	+
		VIII	−	−	−	−	−	−	+	−

The distribution of the clones to the groups and types are shown in Table III.

In the progress of these experiments, no endomixis was found with the possible exception of three clones (C1, C7 and C30). The individuals of these clones on the last

TABLE III

DISTRIBUTION OF THE CLONES TO GROUPS AND TYPES

Group	Type	Clones
1	I	C1–C3, C8–C10, C16, C18
	II	C7, C19–C22
2	III	C4, C11–C12, C25–C26, C33, C40–C41
	IV	C24, C27–C29, C39
3	V	C15, C23, C30–C32, C36–C38
	VI	C5–C6, C13–C14, C17, C34–C35
4	VII	1*b*1, 1*b*2
	VIII	1*a*1, 1*a*2, 18*a*1, 18*a*2, 28*a*1

examination stained very faintly in acetocarmine or methyl green and did not show a distinct nucleus. These three clones were then discarded although it was not definitely established whether they were actually in a state of endomixis.

Structure of Nucleus

Both Feulgen's technique and iron alum hematoxylin were used. The micronucleus stains homogeneously and no distinct chromosomes can be observed. The structure of the macronucleis of all the clones is the same and their sizes are nearly equal.

The structure of the micronucleus shows some variation. In the process of binary fission, the micronucleus is oval-shaped in metaphase. The chromatin material collects in the equatorial region, which stains deeply. The chromosomes are not counted, but their number is not large and they give the same general picture as Penn's figures (Penn, 1937). It may thus be assumed that in this race, the number is the same as given by him (32–38).

In clones C8 and C28, however, the nuclear structure is different from that described above. In C8, the micronucleus is very small and spindle-shaped. It stains very faintly and no distinct chromosomes can be detected in any phase of the binary fission. In C28, on the contrary, the micronucleus is very large and ovoid in shape, with an attenuated end directed toward the indentation of the macronucleus. The chromatin collects at this end, and chromosomes can not be clearly made out.

Thus all the clones except C8 and C28 show uniform structure in the micronucleus. It may be concluded that the structure of the micronucleus gives no indication that it is responsible for sex differentiation.

Discussion

The studies of Jennings (1938) on *P. aurelia* show that there may be many local races differing in mating types and not reacting with races from distant localities. Gilman (1941) studied *P. caudatum* and concluded that there was no evidence for the formation of local groups of mating types which would not conjugate with animals from other localities. Materials for the present investigation were taken from three localities. MA and MB are some 50 kilometers apart, and MB and MC are also about 50 kilometers apart. Yet clones from all three localities are represented in types III, V and VI; those from two localities in types I, II and IV. It is evident that in this investigation locality has no effect on the mating reaction of *P. caudatum.*

Working on *P. caudatum,* Gilman (1941) has reported five groups of animals in nature. But in these studies I have found only four groups of which three were collected from the field and the fourth was raised in the laboratory from the descendants of the exconjugants of group 1. The formation of a new group from exconjugants of another has not been previously reported. Only Jennings (1938) has raised two new mating types of *P. bursaria* from the conjugation between two original mating types. But his two new types belong to the same group as their ancestors, while the two new types I raised form a new group different from their ancestors. This can not be due to reversal of sex (Sonneborn, 1937) because no signs of endomixis have been observed.

In *P. aurelia,* the mating reactions are believed to be determined by the macronucleus (Sonneborn, 1937; Kimball, 1937). In *P. bursaria,* Tartar and Chen (1940, 1941) studied the mating reaction of enucleated pieces and concluded that "the cytoplasm alone (in the absence of the nuclei) exhibits the reactivity and diversity of mating type." In *P. caudatum* it is clear that the micronucleus, as far as its structure is concerned, shows no relation to the mating reactions, since the micronucleus in all the clones except two is uniform in structure. The formation of a new group from exconjugants indicates, however, that the exchange of micronuclear material may have an effect on sex differentiation. It is conceivable that this differentiation may be affected by the interaction of cytoplasm with foreign nuclear material.

CONCLUSION

(1) Mating types are present in the Yunnan race of *Paramecium caudatum*.

(2) Three noninterbreeding groups, each with two opposite mating types, have been identified from the clones collected from the field.

(3) An additional group (group 4), also containing two opposite mating types, has been raised from the descendants of the exconjugants of group 1.

(4) No geographical difference in mating reaction has been found.

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THE ARCHETYPAL POSITION OF AMPHIOXUS AND AMMOCOETES AND THE ROLE OF ENDOCRINES IN CHORDATE EVOLUTION

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I. INTRODUCTION

NUMEROUS and detailed studies on the comparative anatomy and embryology of present-day chordates, together with the evidence obtained from paleontology, have brought into speculative existence an ancestral organism that is useful in understanding the probable phylogeny of modern vertebrate animals. This hypothetical archetype appears to have been compounded out of primitive parts selected from amphioxus, ammocoete (larval lamprey), ostracoderms and various embryos of higher chordate classes. One purpose of the present paper is to reconsider some characters of the hypothetical ancestor as conceived by early investigators with reference to the question—What recent form appears most closely related morphologically?

The principal aim of this review, however, is to consider some aspects of vertebrate phylogeny and ancestry in the light of our present information concerning the profound influence of the hypophysis and the thyroid gland on development. The possible physiologic significance of these organs on vertebrate phylogeny appears to have received very little consideration by modern workers, and of course, such information was not available to the early students who contributed most to our knowledge of primitive forms. A discussion of these physiologic factors will follow a brief survey of interpretations of the archetypal vertebrate based on morphologic data.

General requisites of an archetype: In their classical studies, the early morphologists generally agreed on what the fundamental requisites of a vertebrate archetype should be. To them, the ancestral form possessed an ideal primitiveness combined with sufficient generalization to permit all known divergences to occur, progressively or retrogressively. The progressive advancements could proceed directly without preliminary alterations of the original and fundamental design.

Despite the circumstance that representatives from most of the invertebrate phyla were described as progenitors of the chordates, remarkably similar opinions were held by students of ancestry concerning the problems of form, segmentation, symmetry, cephalization, the character of the central and peripheral nervous elements, the notochord and pharynx of the common ancestor of the vertebrates. Although the early students agreed on fundamentals, many of the more detailed parts of the archetype have been variously described by different authorities to conform with the requirements of the particular invertebrate considered by them to have been the forerunner of the vertebrates.

None of the several theories on the origin of vertebrates from an invertebrate precursor has received much common or popular acceptance. Possibly as a consequence, modern students have neglected a considerable amount of valid and valuable morphologic data merely because they were used in connection with unacceptable hypotheses of vertebrate ancestry. This appears particularly true with concepts of primitive cephalization and structural organization of the notochord and pharynx. The studies made to test the theories of vertebrate origin, however, have not only given us some of our best coordinated accounts of the structure of many interesting animals but a much better (if somewhat confused) understanding of the fundamental requisites of the primitive chordate ancestor of the true Vertebrata.

Related modern forms: Among modern animals, amphioxus and ammocoetes appear most closely related to an idealistic chordate archetype. Most students equally familiar with both types, and acquainted with the vertebrates generally, would probably agree that an amphioxus seems the more primitive and an ammocoete the more generalized. In detailed studies of these forms, however, difficulties are immediately encountered in distinguishing between "degenerate specialization" and "true primitiveness." This is particularly true of amphioxus. However, if we are to employ these forms in the proper reconstruction of an acceptable archetype, distinctions of this sort are obviously imperative.

II. ARCHETYPAL CHARACTERS OF AMPHIOXUS

Present accounts: From a review of modern text-books on vertebrate zoology and comparative anatomy one might assume that most modern authors have accepted amphioxus as the ancestral form of the higher vertebrates as set forth particularly by Willey (1894) and without some of his own qualifications of his theory. Relatively few authors attempt to review other theories of origin. The amphioxus hypothesis appears to have been commonly accepted for two reasons: first, the literature on the descriptive morphology of amphioxus is remarkable for its completeness and excellence, and much of the basic literature was well coordinated and made generally available by Willey; second, the amphioxus theory does not go back to the invertebrates for an ancestor and therefore is not so exposed to attack by the critics of the various hypotheses involving invertebrate phylogeny. These hypotheses, however, concern fundamentally different and more difficult basic problems than does that proposed by Willey.

Although amphioxus has been so generally accepted in text-books as the closest living relative of the vertebrate archetype one could readily consider it as a degenerate divergent type from a common chordate ancestor that gave rise to both acraniates and the craniates. This view proposes that the primitive chordate ancestor not only gave rise to the vertebrate archetype but also gave rise to the small groups of acraniates that did not follow the line of evolution leading to the higher vertebrates. The acraniates in this interpretation, therefore, do not bear a direct ancestral relationship to them. The belief that amphioxus is more degenerate than commonly suspected has been frequently, if not clearly, expressed by several outstanding students of chordate phylogeny, principally by presenting contrary and conflicting evidence regarding its assumed archetypal characters. These contrary evidences have never been well coordinated or publicized. Thus, amphioxus appears to have been over-emphasized by modern authors as a basic ancestral type merely because it clearly possesses primitive characters and structural simplicity. But structural details and organization of the parts presumed to be primitive, and their relation to the whole animal seems to have received inadequate consideration in most of the commonly read accounts of its phylogenetic position and archetypal characters.

Regardless of the difficulties in understanding various hypotheses of vertebrate origin involving invertebrate phylogeny it is surprising that the amphioxus hypothesis has escaped so much valid criticism. The discrepancies in popular accounts are striking in view of the scholarly work on the comparative anatomy of primitive head segments of chordates generally when considered in connection with the excellent specific descriptions of the head of amphioxus. Modern text-books make little or no reference to the many profound studies on primitive head segments. Another puzzling feature that appears to have been given inadequate consideration in text accounts is the highly specialized atrial cavity of amphioxus and its relation to the pharyngeal clefts and gonads, compared with vertebrate conditions. Many other features of amphioxus are distracting in a vertebrate archetype that are scarcely mentioned or insufficiently emphasized by modern authors; examples are: asymmetry of myotomes and spinal nerves; the peculiar histological character of the notochord, its single sheath and the possible significance of its cranial extent; the hundred or more pairs of pharyngeal clefts of the adult which form atypically, open atypically, and incidentally produce a disproportionate reduction of the locomotor region. If one removes the atrium (which is not retained in vertebrates) from amphioxus, some of its more pronounced deficiencies in organization and form as a vertebrate archetype become immediately obvious.

A considerable amount of evidence contrary to the usual acceptance of amphioxus as an archetypal form is contributed by William Patten (1912) in his "Evolution of the Vertebrates and their Kin." Gaskell (1908) in his "Origin of the Vertebrates" also discarded the type as an unsuitable connecting link between the non-vertebrates and the vertebrates. In a more recent account of the "Origin of the Vertebrates," Delsman (1922) gave considerable attention to amphioxus as an ancestral type, but he too had much difficulty with it, and when he dealt with the problem of head segments, referred to the burrowing *Lumbricus* in an attempt to establish homologies. Finally, he, in agreement with most previous anatomists, regarded the brain of amphioxus as degenerate and concluded that "the so-called brain vesicle of amphioxus is not homologous to the brain of the true vertebrates (craniota) but only to the epichordal part of the brain of the latter."

This conclusion is in accord, not only with earlier studies which homologized the "first cranial nerve" of amphioxus with the ophthalmic branch of the fifth of vertebrates, but also agrees with researches in comparative embryology. The developing notochord of all vertebrates consistently extends cranially only to a point just behind the hypophysis. In long extinct fossil forms the notochordal elements can also be traced forward only to the pituitary fossa of the basi-sphenoid bone. Thus the typical forebrain is supported mostly by pre-chordal cartilages.

One may attach further significance to the cranial extent and amount of the embryonic mesochordal tissue that underlies the developing brain by considering the so-called head organizers. According to Huxley and de Beer (1934) in reviewing the original work of Holtfreter (1933) nervous differentiation is induced in axolotls by underlying chordomesoderm. The neural crest is first induced by the prechordal portions of chordomesoderm. If only a narrow portion of the material was present, the overlying cranial neural plate became correspondingly reduced. Not only does the nervous system become reduced in size but develops incompletely and assumes the character of tail neural tube rather than that of a brain. Thus, the lack of pre- and para-chordal cartilages in the head of amphioxus may help explain the condition of the "brain" of amphioxus as resembling a reduced neural tube.

From the evidence of comparative anatomy of cranial nerves, the conclusion must be reached that both fore- and mid-brain in amphioxus is missing. Since none of the "head" of amphioxus is prechordal, the evidence from embryology clearly shows that were these brain parts to form in the characteristic vertebrate manner they would necessarily have to develop mostly as an extension beyond the present cranial limits of the animal. Therefore, it seems incredible that the brain of amphioxus is primitive and could evolve into a brain morphologically comparable with that of lower vertebrates or approach the condition reached in the early development of any true vertebrate.

One other source of evidence may be cited which is in accord with the views of the comparative anatomists and embryologists concerning the degenerate character of the head of amphioxus. That is the evidence provided by fossil forms of the earliest known chordates, the ostracoderms. These forms had well-defined heads and while they may not have antedated possible amphioxus-like animals which were not preserved as fossils, they definitely indicate that the lack of head parts is not necessarily a primitive character. Gregory (1933) assumed these forms to represent the basic position in his discussion of the essential stages in chordate phylogeny and he completely ignores amphioxus as an ancestral form.

The conditions that originally started amphioxus on its degenerative line of evolution is, of course, subject to more speculation than an account of the probable sequence of events that would follow the loss of the forebrain and hypophysis. Amphioxus-like types must have antedated the earliest chordates of which we have fossil records; *i.e.*, the armored ostracoderms. Whether the amphioxus type once possessed this armor, or never did acquire it, does not seem important here. However, the soft-bodied forms probably began their burrowing habits relatively early in phylogeny, to escape their more formidable relatives. The loss of sense organs may be regarded as being associated with the semi-sedentary habits of the animal in a darkened environment. Degenerative changes of the olfactory and optic structures if sufficiently extended would lead to the obliteration of olfactory lobes, optic thalamus and optic lobes or midbrain of lower vertebrates and thus cut off practically all functional demands of any parts craniad to the hindbrain. The necessity of a pointed and extended notochord would appear more urgent in an animal with the burrowing habits and environment of amphioxus than the presence of pre- and parachordal cartilages and expanded forebrain. The phylogenetically significant point here would appear to be the accompanying loss of the hypophysis, the master regulating mechanism so essential to advancement of vertebrate characters.

III. ENDOCRINE FACTORS AFFECTING AMPHIOXUS

In discussing the acraniates, William Patten (1912) appears to have made a profound and prophetic observation: "There is a strong tendency in the entire group toward a retrograde or degenerate development that appears to be due to some prevalent lack of internal conditions or of materials. It makes its appearance during or shortly after the larval stages, cutting down the first promise of a clear-cut, vigorous organology to one that is feeble, blurred or defective in definition; or one in which important parts are lacking.'' Here, Patten clearly expresses the opinion that physiologic factors in amphioxus (as in other acraniates) are responsible for the peculiar morphology they exhibit as adults and the atypical and devious developmental path they all follow in reaching the so-called adult condition.

In the light of present information on the physiology of the hypophysis and its thyrotrophic function, the statement of Patten might well be expanded to read somewhat as follows: With the absence of the more cranial head parts, including the forebrain and hypophysis, both nervous and chemical directive forces in amphioxus and other acraniates were critically impaired. The preclusion of thyrotrophic properties within the animal has prevented a typical development and differentiation of the thyroid gland. As a result, the thyroid complex (endostyle) followed a degenerate line of evolution and has lost its capacity to produce the hormones necessary for vigorous growth and metamorphic changes leading to an advanced phylogeny. The lack of these internal materials and conditions has resulted in a defective and feeble line of evolution away from the vigorous vertebrate line. Of all the acraniates, amphioxus (Cephalochorda) alone has succeeded in retaining some little resemblance to the vigorous ancestral stock from which they and the higher chordates have come. But none of the acraniates meet the requirements of a vertebrate ancestor. Their degenerate morphology and peculiar developmental history is about what one would expect in view of modern experimental data concerning organizers and the pituitary and thyroid glands.

IV. AMMOCOETE AS AN ARCHETYPE

The most complete account of the morphology of an ammocoete in English is that of Gaskell (1908). This account is not coordinated, however, and is used in connection with a theory of vertebrate origin that was subjected to considerable ridicule. Regardless of the use to which the morphologic data was put, it includes a considerable amount of careful and accurate description of ammocoetes, much of which is original. Gaskell was convinced that earlier morphologists were correct in their opinion of its archetypal fitness, but many of his conclusions concerning invertebrate homologs are unacceptable. This is one of the striking examples of how valid data on the ammocoete are commonly unknown and unread because they are associated with an unpopular hypothesis. Almost all modern text-book accounts of ammocoetes are fragmentary and inaccurate apparently because of the uncoordinated and fragmentary character of the literature. In view of the commonly accepted phylogenetic position of the form, it is surprising that more effort has not been made by modern authors to present a more adequate and accurate account of it.

The larval form of all lampreys is known as the ''ammocoete'' stage because of the early misconception which regarded it as an adult cyclostome, and resulted in its classification as *Ammocoetes branchialis.* An ammocoete is unique in many ways, but the most striking morphologic feature of the animal is the prolonged retention of many structural characters which are present only during the embryologic differentiation of vertebrates generally. The transformation of ammocoetes, therefore, involve what might be looked upon as a long delayed completion of an interrupted embryonic differentiation which had been prematurely overpowered by dominant growth factors.

In comparison with larval forms of other vertebrates (amphibians) the ammocoete occupies a fundamentally different plane of development. Whereas, the definitive histologic pattern of the thyroid and pituitary glands are fairly well established as embryonic features in frog tadpoles, the formation of thyroid follicles and striking hypophyseal changes are concurrent with general metamorphosis in ammocoetes. This event in lampreys is several (possibly 4 to 7) years post-embryonic. Thus ammocoetes pass through a prolonged pretransformation growth period with partially developed endocrine organs. Other delayed differentiation that is embryologic in other vertebrates concerns "tubular muscle" of the pharynx, migrating germ cells and the retention of a rudimentary eye.

From the standpoint of comparative anatomy, ammocoetes has long been regarded as the modern form standing nearest to an ideal archetype by leading students of vertebrate phylogeny. Although William Patten (1912) put particular emphasis upon ostracoderms, his material did not allow the extended observations as did the more recently discovered fossils which are monographically described by Kiaer (1924) and Stensiö (1927). These show the ostracoderms to be remarkably similar to the ammocoete with the exception of the exoskeletal armor.

Ammocoetes as unarmored ostracoderms: Some archetypal characters of ammocoetes may be better understood by quoting from Gregory (1933) in his review of stages in vertebrate phylogeny. Writing of the ostracoderms described by the Scandinavians, he stated: "Beneath the braincase was a greatly expanded chamber containing the mouth cavity, the gill pouches, the skeletal partitions between the gill-pouches and the ducts leading to and from the gill openings and the exterior. The arrangement is closely paralleled in the larval stage of the existing lampreys. The same is true of the brain and cranial nerves. The neurologists and students of the classical problem of vertebrate head segments had long ago fixed upon the larval stage of the lamprey as standing nearest among existing forms to the archetypal vertebrates. Thanks to the labors of many investigators, we can now affirm that the ostracoderms as a class were the archetypal vertebrates from which were derived, on the one hand, the so-called jawless cyclostomes, or lampreys and hags, and on the other hand, the gnathostomes, or jaw-bearing vertebrates, comprising true fishes, amphibians, reptiles, birds and mammals (including man).''

In view of the above statements, it seems a little puzzling that Gregory did not give more consideration to the ammocoete in the basic phylogenetic position in his scale rather than emphasize the more highly specialized ostracoderms. Presumably he attached considerable importance to the age of these fossil forms and did not care to assume the existence of an unknown soft-bodied animal giving rise to an armored type which became soft-bodied again by losing these parts. But certainly the type of exoskeleton possessed by ostracoderms is not in line with advanced phylogeny, unless the armor plates are regarded as forerunners or homologs of the smaller and more numerous scales of other fishes. One might consider the possibility that some early chordates passed through the complete age of ostracoderms without developing parts to become fossilized.

The backward character of the ammocoete eye might appear to be discordant in an archetype. The same is true with reference to the dorsally located and atypical naso-pituitary opening similarly placed in the ostracoderms. We shall first consider the eye.

A curious and generally unknown phase in the development of the eye of ammocoetes may have phylogenetic significance. In his exhaustive study of ''The Vertebrate Eye,'' Walls (1942) redescribed a patch of functional visual cells which develop embryologically in ammocoetes as ''Retina A,'' but lose their function when the young larva burrow in the sand and mud. Then at metamorphosis (several years later) ''throughout the remainder of the much expanded retina ('Retina B') the visual cells are suddenly differentiated and the borders of Retina A become indistinguishable. Retina A goes out of function when the young larva first burrow in the mud and the eye is blind until metamorphosis when the skin covering becomes transparent and Retina B matures.'' Walls further points out that Stŭdnicka's theory of the primitive eye "laid great stress on the eye of the young larval lamprey which is precociously functional while still merely an optic vesicle, as indicating that the vertebrate eye was originally merely a 'directional' one before it became capable of forming images. Since the lens is already present in the tiny lamprey, but in the form of a flat cushion incapable of dioptric function, Stŭdnicka argued that it must have existed phylogenetically a vestigial remnant of something else, possibly a sense organ before the retina was devised at all." One might speculate on the possibility that the onset of the burrowing habit in ammocoetes represented not only a critical period in the life-history of ammocoetes but also had a significant relation to the subsequent phylogeny of other chordates, which unlike ammocoetes did not burrow in the mud. The appearance, disappearance and reappearance of similar function in a developing organ does not seem to be paralleled among any other vertebrates.

Students of the comparative anatomy of the anterior pituitary have traced this organ phylogenetically to a "hypophyseal pit" on the dorsal aspect of the head of cephalaspid ostracoderms, in a position that corresponds to the nasopituitary opening of modern cyclostomes. The primitive position and extrabuccal origin of the anterior pituitary is reflected in its development in amphibians, in which the anlage moves from an original dorsal position to a more ventral one. These observations indicate that the more usual mode of origin of the anterior lobe in vertebrates (from buccal ectoderm) has been secondarily acquired from an Ordovician ancestral form that possessed a well-developed pituitary complex, and that the condition in cyclostomes is essentially primitive rather than degenerate. Homologous features in acraniates, if present at all, are extremely obscure and must be based on meager and questionable evidence. The comparative anatomy and physiology of the pituitary has recently been reviewed by Gorbman (1941b).

V. PROBABLE ROLE OF ENDOCRINES IN EVOLUTION

Development of adequate thyroid tissue would seem to be essential not only to the proper development of the individual but also to the advancement of the entire race of vertebrates. The most striking differences between the endostylar organs of acraniates and ammocoetes involve the number and character of cell types and the gross morphologic pattern. In my analysis (1939) of the homologies in endostylar organs, the types of cells most active in the formation of thyroid follicles in ammocoetes are either entirely lacking in acraniates or have been so altered as to obscure their phylogenetic relationship. Of the six types of cells making up the endostylar apparatus in ammocoetes only two (possibly three) are even present in amphioxus. In functional morphology, the endostyle in acraniates is obviously a ciliated tract concerned with propelling food through the pharynx, whereas the endostyle proper of ammocoetes is to be regarded as a primitive pouch designed for the intake and circulation of water over a large absorptive area. The design in ammocoetes suggests that the organ is utilized to absorb essential dissolved minerals from the water which may be concentrated and stored in its tissues (Leach, 1939). Despite text-book repetition, there is no clear functional agreement between the endostyle of amphioxus and that of ammocoetes, and the usual statement that the endostyle of ammocoetes is phylogenetically intermediate between the acraniate endostyle and the thyroid of true vertebrates is to be seriously questioned. The view that the endostylar apparatus in all acraniates are specialized remnants of an earlier generalized structure leading directly to the vertebrate thyroid would appear just as valid and understandable.

Recently, Gorbman (1941a) has shown that the endostyle of the ascidian, *Perophora annectens,* does not store iodine but that the stolon is capable of iodine accumulation in a degree comparable with vertebrate thyroid. He, with Dr. Creaser (1942), has further shown that the endostyle of ammocoetes does accumulate iodine; and that the endostyle of amphioxus and of two other ascidians do not. The circumstance that the stolon of the ascidian is a reproductive organ and usually arises in ascidians from the pharyngeal endoderm in the region of the endostyle is of particular interest. I have frequently observed migrating germ cells in the mid-dorsal fold of the pharynx of ammocoetes above the epipharyngeal groove, which is a part of the endostylar complex. This may be a morphologic clue to the functional relation of the thyroid to the reproductive glands.

VI. Discussion

The few experimental studies which have been made on the endocrines of the lower chordates have yielded few important positive results. My own observations (unpublished), together with those of others, show with certainty that ammocoetes do not respond to thyroid treatment after the manner of amphibian larval forms either as to metamorphosis or metabolism. But, as was previously set forth, the larval lamprey is not provided with similar structure, so that parallel results from similar treatment should scarcely be expected. My opinion is that the endocrine glands, such as the thyroid and anterior pituitary, which possess multiple properties have developed their fractions or properties progressively and phylogenetically and that these properties operate only in particular combinations. Although there is little experimental evidence to support this view, some significance may be attached to my observations that normal metamorphosis occurs in lampreys without any increase in oxygen consumption. Thus one may assume that a fraction of thyroid concerned with metabolism is either not fully developed or that the lamprey is capable of responding only to fractions concerned with growth and metamorphosis, and to the latter only at a critical and peculiarly delayed period in the life history. Recent observations by Smith and Everett (1943) support earlier opinions that the metabolic property of thyroid is also not present in teleosts. Etkin (1934) also presented data discordant with the usual opinion that the thyroid gland produces an increase in the oxygen consumption of frog tadpoles but used a different basis of computation than previously used. These studies would appear to be of phylogenetic interest.

This review should not serve to discredit amphioxus with reference to its clearly primitive characters and simplicity of structure. To accept it as an archetype of the vertebrates, however, seems to be a different matter and requires more detailed analyses than have been made. The review definitely supports the opinion that amphioxus should be regarded as a persistent and paedogenic larval form that has undergone a considerable amount of so-called degenerate specialization probably associated with its burrowing habits. To the believer in the recapitulation hypothesis who follows through the complete developmental history of amphioxus, the conclusion would certainly be reached that many periods occurred in its phylogeny when "it had no idea as to which tree it was climbing."

Incidently, the present paper should add emphasis to the recognized need for a modern and extensive monographic account of the lampreys which would include a redescription of the detailed morphology of ammocoetes and a full account of the transformation process. Many of the difficulties one encounters in working with these animals, along modern lines, is referable to the uncoordinated and often fragmentary information that has been published concerning them and the necessity of getting much of it first hand.

SUMMARY

(1) A review of the opinions of leading students of comparative anatomy and phylogeny of the vertebrates shows that they were remarkably consistent in regarding amphioxus as an unsuitable archetypal chordate, and looked upon it as a degenerate type entirely off the line

of vertebrate evolution. This is discordant with most text-book accounts.

(2) Much of our information concerning ammocoetes has been used by investigators of phylogeny in constructing an idealistic archetype acceptable to them as a chordate connection with invertebrate progenitors. The unpopularity of the various hypotheses is apparently responsible for the present lack of knowledge of the ammocoete and its archetypal characters.

(3) Physiological evidences support the view that amphioxus is extremely degenerate. From a review of studies on organizers and endocrines, the morphologic characters of amphioxus are remarkably similar to a predicated condition based on analogies from experimental work.

(4) The conclusion is made that a sequence of dependent events occurred in the phylogeny of amphioxus initiated by the loss of head parts.

(5) Loss of the pituitary is regarded as particularly significant in leading to a degeneration of the thyroid gland (endostylar complex). Degeneration of thyroid apparatus is reflected in the peculiar development of amphioxus and morphologic deficiencies of acraniates in general.

(6) Since the thyroid gland is so characteristic in all vertebrates and largely responsible for the regulation of growth, differentiation and metabolism of higher forms, its preclusion of function would terminate advancement in phylogeny as in ontogeny.

(7) The review proposes that endocrines possessing multiple properties of independent character have developed these fractions phylogenetically and in a progressive manner. This hypothesis has not been tested very fully.

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GEOGRAPHICAL DISTRIBUTION OF THE GENUS *PYRUS* AND TRENDS AND FACTORS IN ITS EVOLUTION

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ACCORDING to paleontological data, the genus *Pyrus* (the pear proper) is of Tertiary or, possibly, even more ancient origin. Tertiary remains (leaves) have so far been found only in a few localities of western Europe and the Caucasus. In western Europe—in Miocene deposits at the famed site of Tertiary remains, the village of Parschlug in Steyrmark, Austria—Unger found and described the fossil species, *Pyrus theobroma.* In the Caucasus, according to Palibin, *P. theobroma* is found in eastern Georgia in the Kakhetia Mountains in Middle and Lower-Middle Sarmatian deposits, together with representatives of a mixed flora including a considerable number of evergreens, which attests a subtropical or, at least, a warm climate. *P. communis* L. is found in eastern Georgia in Upper Pliocene deposits in the Akchagyl horizon and in Azerbaidzhan in the Apsheron horizon. In all cases these fossil remains are found among representatives of a warm, temperate climate, together with numerous species identical to present-day forms. Post-glacial remains of the pear (fruits) are known in lacustrine deposits in Switzerland and Italy.

In contrast to the closely related genera, *Malus* and *Crataegus*, which belong to the so-called "arctic-Tertiary" flora and have, like other members of this flora, representatives both in Asia and North America, the genus *Pyrus* has no fossil occurrences in North America. This specificity in the location of fossil remains of *Pyrus* and the peculiarities of the present geographical distribution of the genus indicate that it originated at a later date than the other genera mentioned and in a different geographical region.

The species composition of the genus *Pyrus* has not yet been definitely established. The number of species increases as further special investigations are made. According to the latest taxonomic works,[1] there are as many as 60 different species names for described forms, which number, however—after discarding duplications and reducing many to the rank of varieties—falls to 25. To these there should be added *P. gharbiana* Trab. and *P. mamorensis* Trab. (from North Africa) and a number of new species discovered in recent years in the U.S.S.R.

During the past fifteen years there have been revealed in the Caucasus and Soviet Central Asia centers of remarkable diversity of pears, and there have been discovered several new species in these regions. Voronov has described three new species in the Caucasus—*P. Raddeana, P. taochia* and *P. oxyprion;* Popov—two hybrid species in Soviet Central Asia, *P. Vavilovii;* Maleyev—*P. zangezura* in southern Armenia and *P. turkomanica* in the Kopet-Dagh Mountains; Fedorov—two species in southern Armenia, *P. Grossheimii* and *P. Takhtadjanii* and one species in Lenkoran, *P. Sosnovskii.* During very recent years the writer has described five new species from southern Armenia: *P. elata, P. nutans, P. Voronovi, P. Medvedevi* and *P. complexa.*

After a critical study of the genus there remain at least 35 species, differing from one another in regard to the number of varieties and forms they comprise, the complex of characters they possess and the degree to which these characters are expressed, and their antiquity and areas of distribution.

The species diversity of pears is concentrated in two regions of the globe—western Eurasia and eastern Asia, chiefly China. In these two regions there were formed two distinct groups of species and cultivated forms of pears—western and eastern. The former includes over

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[1] C. K. Schneider, Illustr. Handb. d. Laubholzkunde, 1906; Rehder, Manual of Cultivated Trees and Shrubs, 1927; Index Londinensis, 1933.

20 species, found in Europe, northern Africa, Asia Minor, Iran, Soviet Central Asia and Afghanistan. To this group belong most of the cultivated pears of the globe. The second group embraces from 12 to 15 species concentrated in eastern Asia, from the Tien-Shan and Hindu Kush Mountains to Japan. To it belong a very large group of varieties cultivated in China and Japan.

The geographical distribution of the various species shows that the genesis and dispersal of the genus *Pyrus* took place in ancient times over an immense territory, extending from eastern Asia to southern Europe and northern Africa. Taking into consideration the areas of the various genera of *Pomoideae*, it seems very probable that their common progenitor was widely distributed over this territory in the Cretaceous period or, at any rate, in the Paleocene epoch (early Tertiary).

The most probable place of origin of the genus *Pyrus* is the mountainous region (on the border between the north temperate and tropical zones) in western and southwestern China, where, according to recent investigations (Wilson and others), there is concentrated an exceptional wealth of genera and species of *Pomoideae* and *Prunoideae*—a region that may well claim to be the primary center of origin of the floras of Asia and Europe, as Komarov (1908) noted in his work, "Introduction to the Floras of China and Mongolia."

Beginning with the Tertiary period, as has been established, an exchange of floras was possible between Interior Asia (including central Asia), on the one hand, and the Caucasus, Asia Minor and the western regions of the Old World, on the other.

Living evidence of the dispersal and evolution of the genus *Pyrus* in ancient times is found in the form of relict species, at present geographically isolated but characterized by certain common features of a primary character. These include: *P. longipes* Coss.-Dur. in the Atlas Mountains (Algeria and Morocco), *P. Boissieriana* Bse. at

Talysh in the Kopet-Dagh Mountains and *P. cordata Desv.* on the Atlantic coast (France, England), all characterized by fruits having a deciduous calyx, being similar in this respect to the East-Asiatic species, *P. Pashia* Ham.-Don., *P. serotina* Rehd., *P. betulaefolia* Bge., etc. Or let us take another example. The xerophytic species of Anterior Asia and Soviet Central Asia—*P. glabra* Boiss., *P. heterophylla* Rgl. et Schmalh., *P. bucharira* Litw.—and the East-Asiatic species are likewise geographically and especially ecologically isolated, but their affinity is, nevertheless, established by the fact that they possess the following characters in common: dissected leaves, ovary with few locules.

Paleontological remains of the genus *Pyrus* and of closely related genera from the period of the great mountain-forming processes in Asia, Europe and Africa and the connection of the past area of the genus with the chief mountain systems of these continents give grounds for linking the development and dispersal of the genus with the formation and location of these mountain chains. The fact that the latter run east and west led to the genus dispersing in the same direction. Deserts, seas and snow-covered mountains constitute insuperable barriers to the natural dispersal of the genus. Only in foothill and adjacent regions are there found, on the one hand, a great diversity of ecological conditions favoring form-genesis and, on the other, a certain uniformity in average conditions (climatic, edaphic) that makes possible the unimpeded dispersal of forms. Convincing facts in favor of this view we find, for instance, in the distribution and localization of the diverse forms of *P. salicifolia* Pall., *P. elaeagrifolia* Pall., and *P. syriaca* Boiss, in the U.S.S.R.

P. elaeagrifolia grows on the northern and southern foothills of the Crimea, extending on the east to the Kerch peninsula, but it is not found in Novorossisk District, which territorially and floristically is so close to the

Crimea that it belongs to the same botanical province. The steppes and the narrow expanse of the Azov Sea constitute an insuperable barrier to the spread of this species. *P. salicifolia,* which grows in the Caucasian foothills, has extended its range from Armenia into Georgia, Azerbaidzhan and Daghestan, but it is not found either in the steppes or in humid forest regions in the mountains. *P. syriaca* is distributed, in a great diversity of forms, only in the middle altitudinal zone in Zangezur and Daralagez (southern Armenia).

The western group of forms extend as far east as the western Tien-Shan, Pamir and Hindu Kush Mountains. The Himalayas constitute a bridge between the western and eastern regions of species diversity of this genus. Here we find a member of the eastern group, *P. Pashia,* having migrated hither from China. This species, with respect to a whole number of morphological characters, may be regarded as an intermediate link between the eastern and western species. Of all the eastern species it is the closest to *P. communis* and *P. Korshinskyi.*

On the basis of our botanico-geographical study of the genus *Pyrus,* we may draw the following conclusions as to the genetic relations and comparative antiquity of the principal species.

The most ancient species, still preserving primitive features, are the Chinese—*P. serotina, P. Calleryana, P. betulaefolia* and others. *P. Pashia* constitutes a connecting link between the relict species, *P. Boissieriana* and *P. longipes* (which are close to *P. communis*), on the one hand, and *P. Korshinskyi,* on the other. Close to the latter, morphologically and biologically, are the xerophytic species of the Iran group—*P. heterophylla, P. glabra* and *P. salicifolia*—and the species of Asia Minor and the Mediterranean Basin—*P. syriaca, P. elaeagrifolia* and *P. amygdaliformis* Vill. *P. Korshinskyi* is undoubtedly linked with the Iran group by way of *P. heterophylla* and with the Asia Minor group by way of *P. syriaca,* the exceptional similarity and closeness of which were noted by Litvinov.

The most recent branch in the evolution of each of the three main, primitive groups of pears we consider to be as follows: Group I (Chinese), *P. ussuriensis* Maxim.; Group II (*P. Boissieriana, P. longipes*), *P. communis;* Group III (Iran and Asia Minor), *P. nivalis* Jacq., close to *P. elaeagrifolia,* probably a variety of the latter.

Taking into account the present geographical distribution of *Pyrus* species and the generally accepted views on the chief factors involved in the development of floras, it must be recognized that the evolution and species differentiation of the genus are based primarily on processes of xerophytization and borealization. These processes, particularly the former, have been operative over a prolonged period of time and over great expanses of territory in the southern part of the area of the genus. Hence, the great diversity of species of pears in the region of the ancient Mediterranean. From the beginning or middle of the Tertiary period the extent of dry land in this region began to increase, and there were formed centers of xerophytic forms—Central Asiatic, Iran and Asia Minor. In these centers there developed, corresponding to the diversity of physiographic conditions, a large group of Mediterranean species, to which the Central Asiatic species may also be referred.

The diversity of climatic conditions in this region and their close similarity to those prevailing in ancient times have led, on the one hand, to the creation here of great genotypic diversity and, on the other, to the preservation and development of relict types less specialized genetically. In the Anterior-Asiatic center, particularly in southern and southeastern Armenia (Daralagez, Zangezur), there have been discovered modern centers of species-formation in *Pyrus.* The species, *P. syriaca* and *P. amygdaliformis,* which are found in Anterior Asia and along the shores of the Mediterranean, are in a stage of intensive form-genesis; due to their polymorphism and morphological instability, they present many difficulties to the taxonomist. The species, *P. salicifolia, P. heterophylla* and *P. glabra,* which are biologically more specialized, are extreme xerophytic types, polarized, so to say, genotypically.

As examples of the effect of the process of borealization we may cite *P. communis* and, probably, several forms of *P. elaeagrifolia* (*P. nivalis* Jacq.). As compared with southern species, the European *P. communis* is characterized by great uniformity. The diversity of this species found in several countries of western Europe, *e.g.,* in France, can not be compared with the polymorphism of *P. syriaca* and *P. amygdaliformis,* and has arisen, no doubt, as a result of hybridization with cultivated forms. It should be noted that even *P. communis* is most polymorphic in Central Asia, Transcaucasia and Asia Minor, *i.e.,* in the region of the ancient Mediterranean. This is confirmed by historico-geographical data. The present-day representatives of *P. communis* in Europe are of comparatively recent origin, and they all arose under like conditions of borealization. The ancient representatives either have died out or have been preserved in the south, where they have undergone a more prolonged period of differentiation under more normal conditions. It is remarkable that it is precisely the Transcaucasian forms of *P. communis* that are closest to the relict species, *P. Boissieriana* and *P. longipes.*

Analogous relations may be observed in the East-Asiatic group of species, with this difference, however, that the process of xerophytism has left less imprint, while the process of borealization has been more prolonged and produced more effect. As a result, in the northernmost part of the area of this group, in Manchuria and the Amur and Ussuri Basins, there has developed a boreal species, *P. ussuriensis* Maxim; in the northwestern part, adjoining the Central Asiatic (Mongolian) arid center, there have developed types with xerophytic features —*P. betulaefolia* Bge., *P. phaeocarpa* Rehd.; in the central part, where conditions are closest to those of ancient times, there has developed a large group of species of the type of *P. serotina* Rehd.; and, lastly, in the southern and southwestern part, bordering on the subtropics, a form transitional to the evergreen type, *P. Pashia* Ham.-Don.

P. ussuriensis Maxim. constitutes the most specialized branch of the East-Asiatic group, being characterized by the same degree of elaboration and divergence as most species of the Manchurian flora. This species originated in a more ancient period than the European *P. communis.*

In the present epoch one of the most important factors in species- and form-genesis in *Pyrus* is hybridization. More than six hybrid species have been described. By a study of the wild species in Soviet Central Asia, the Caucasus and the Crimea the writer has established the existence of numerous interspecific hybrids, some of them composite hybrids. In places where areas overlap and where in general there is found the greatest species diversity there is concentrated an amazing diversity of forms of *Pyrus, e.g.,* in southern Armenia and western Tien-Shan.

Particularly great is the rôle of hybridization in the origin of the diversity of cultivated varieties. By a comparative analysis of wild and cultivated forms of *P. communis* it has been found that some cultivated varieties of this species possess characters, particularly leaf characters, indicating the participation in their heredity of other species, *i.e.,* the hybrid origin of ancient types. Thus, as regards the shape and texture of the leaves, the character of dentation of the leaf margin, and the size, color, shape and pubescence of the buds and shoots, in some cultivated varieties of *P. communis* we may detect characters of *P. syriaca, P. Korshinskyi, P. salicifolia* and *P. elaeagrifolia.* A number of cultivated varieties have in recent times been created by interspecific hybridization with the participation of *P. ussuriensis* and *P. serotina.*

As a result primarily of natural and artificial intervarietal hybridization, there has developed during the past two centuries an enormous varietal diversity of cultivated pears. For the radical improvement of the pear with respect to winter hardiness, disease resistance and ecological adaptability pear breeders now have at their disposal a great diversity of initial material. In hybridization work there may be utilized representatives of different species possessing valuable biological properties.

Interspecific hybridization, as in the case of other plants, induces intensive processes of form-genesis and accelerates evolution in new directions.

REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

In these section reviews and notices of current publications on general biology emphasis is given to books and major articles which fall within the special scope of The American Naturalist, in that they deal with the factors of organic evolution. Reviews and Comments are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

Mankind So Far. By William Howells. Garden City, New York: Doubleday, Doran and Co. (Am. Mus. Nat. Hist., Sci. Ser., 5), 1944: i–xii, 1–319, 7 pls., 37 figs. $4.50.

It has been said that the anthropologist is most competent to appraise the past, present and future of man. Certainly his appraisal is worthy of consideration, particularly when it is set forth, as it is by Howells, in a thorough yet fascinating way. A particular virtue in this book is the presentation of findings on hominid evolution that were so recently published or so technically presented as to have escaped the attention of all others than specialists, and perhaps some of them.

Principles of phylogeny and speciation are continuously made the basis for judgment on the ancestry of man and on the course of human evolution. This background biology, which is of prime concern to us, is a mixture of good and bad, with the good predominating in matters of real importance. Thus a strong contrast is rightly drawn, as Kinsey did for gall wasps, between the insular and the continental types of speciation in man. The evolutionary potential of the generalized and the limitations of the specialized are often well expressed. Nevertheless, the bizarrely specialized ostracoderms are placed, on the authority of certain leading students of vertebrate evolution, to be sure, near the base of the vertebrate stem leading to man.

The carrying backward of several phyletic lines well toward the ancient, generalized root, within the human species, within the genus *Homo,* within the Hominidae and within the Primates is quite in line with the trend in phylogenetic research. Yet the course of evolution is repeatedly portrayed as on the plan of a spruce tree, despite the fact that the interpretations preferred would have been much better expressed figuratively by a deliquescent rather than an excurrent tree; even better by many-stemmed shrubs connected by runners. The possible polyphylety of *Homo sapiens* is considered, but hardly favored.

The importance of the natural selection principle in "The Origin of Species" is stressed as Darwin is elevated on a high pedestal, but in the next breath selection is held to be no longer accepted by naturalists generally as the main key to evolution. "There is actually no evidence or explanation," we read, "for the phenomenon of adaptation." Obviously, Howells has failed to appreciate the extent of the swing toward Neodarwinism which has been expressed during the last decade, not only by naturalists, who never wandered far from the fold, but also by geneticists. Evolution, of course, is taken for granted as a fact.

Orthogenesis and Lamarckism are rejected rather thoroughly, but the evolutionary facts which have given rise to such theories are left unaccounted for. The rather ready explanation of these facts on the basis of selection are not given due consideration. There are hints of a predestinational philosophy.

The treatment of anthropological facts appears to be accurate and the presentation of the conflicting theories based on these data seems to be conservative and judicious. Erroneous and doubtful statements noted by the reviewer are largely in biology. We are told, to cite examples, that man is the newest animal; that lungs, warm blood and the human brain are not specializations; that roundworms have been selected, because they are segmented, as ancestral to vertebrates; that amphioxus is only "inch-long"; that the fauna of Celebes is essentially Asiatic. Some of these mistakes could have been eliminated, had a broadly trained biologist read the manuscript. Some minor misstatements are attributable to imaginative and dramatic presentation, which though effective should never be allowed to transgress or distort accuracy, even in details.

Human races are treated at some length. Hybridization is relied upon to explain the characters of many local types, though the modern concept of reticulate evolution is not strongly emphasized. Taking part in the swing away from super-race philosophies, Howells all but denies the existence of any racial differences in mentality. The superficial physical differences between stocks are, even more oddly, ascribed to nonadaptive evolution. In limiting adaptation to specific differences the claims of many biologists are transposed. I favor the view that most racial as well as most specific differentiae are of adaptive significance.

In the final, rather anticlimactic chapter, "1492 to 1,000,000 A.D.," the anthropologist takes a look forward. He foresees the possible further loss of head hair and the chance that man may eventually become bereft of his little toe, but in between almost completely ignores mankind's greatest problem: how to forestall the tendency toward degeneration which, unless somehow checked, may on biological grounds be expected to follow our release from many of the rigors of natural selection.

The Sources of Life. By SERGE VARONOFF. Boston: Bruce Humphries, Inc., 1943: 1–240, figs. 1–47. $3.50.

To Serge Varonoff the sources of life are the glands of internal secretion, particularly the sex glands; they are the seat of energy and well-being; their reduced functioning leads to senility, which, before some such age as one hundred, is pathological and avoidable. The author's remedy is the grafting of endocrine glands, by special techniques that are said to insure the continued functioning of the transplanted tissues. For operations on man, the glands of other primates are used.

The critical reader will find many reasons for doubting part of the claims that the hand of time may be turned backward for man by the monkey-gland operation. The attempted demonstration is by the precept of example, without sufficient statistical analysis to make it certain and obvious that the successes recorded are attributable to the grafting of simian testes. Since many of the operations involve the transplantation of the thyroid and other endocrine glands in addition to the sex glands, the particular role of the grafted testes is obscured. Failures up to "5 to 12 per cent." are admitted, and no real proof is given that the average case is substantially benefited. Some of the before-and-after pictures are very striking, but others are less convincing. The one case in which hair is claimed to have been restored is illustrated by photographs of a man who appears much balder after than before the operation (Figs. 38 and 39).

The most spectacular claim, from a biological standpoint, is that the offspring of grafted rams yield an increased amount of wool. In Algeria the sheep thus magically endowed with hair-growing power are claimed to be the only ones that grow wool on their bellies. These are among the few claims supported by actual figures, but the data are hardly precise. Dr. Varonoff envisions an enormous increase in the wool crop through gland operations on the rams. "We are at the dawn of a new era," he exuberates, for he expects to "create, by grafting, a new race endowed with longer and more abundant wool." He makes no definite claim that the human race can be similarly improved through gland transplants on men, but he hints at such a belief in quoting the experience of a disciple. The spectacular results which he has obtained with thyroid transplants on myxoedematic idiots seem unquestionable. That the energy of senile animals and even their reproductive capacity have been restored and carried several years beyond the normal span of life seems proved for at least some of the gland operations, but to accept the claim that the descendants of a grafted male will be greatly affected stretches the biological mind beyond the limit of elasticity.

The demonstrated persistence and long-continued functioning of some of the simian gland transplants in man provides further evidence of the close relationship between *Homo* and the great apes and other primates.

Dr. Varonoff writes with convincing sincerity, rising occasionally to the spirit of a Messiah: "I have responded to the needs of the world. I have opened a new prospect." His convictions are obviously so strongly rooted as to push aside, at times, the firm ground of scientific criticism.

NOTICES OF NEW BOOKS

Elements of Biology A Brief Course for College Students. By PERRY D. STRAMBAUGH AND BERNAL R. WEIMER. New York: John Wiley and Sons, 1944: i–vii, 1–461, figs. 1–208. $3.25.—"Of the making of biology textbooks," the authors admit, "there is no end." In this one, "there are two general objectives. First, there is the presentation of certain basic principles. . . . Second, there is the incorporation of the fundamental information that will contribute to better living and more efficient participation in the affairs of society." In these worthy aims the authors have been successful. It is clear that "integration of the material used has been obtained by lining up the facts on a functional thread," but the authors have not consistently "followed the pedagogical course of proceeding from the known to the related unknown." The first factual material, on the physico-chemical constitution of matter, on cell structure, and on plant physiology is not ground that the elementary student has trod. Classification is almost eliminated, and I am particularly disappointed to find only a dozen lines on fishes. Although applied biology is commendably stressed, conservation is very inadequately treated. The discussions of soil erosion, conservation of water, and forestry are very brief, and the treatment of wildlife is even less adequate, for it is confined to eleven lines and leads off with the disproven idea that forests are "the natural home of wild life."

A Text-Book of Histology Arranged upon an Embryological Basis. Sixth Edition. By J. LEWIS BREMER. Rewritten by HAROLD L. WEATHERFORD. Philadelphia: The Blakiston Co., 1944: i–ix, 1–723, figs. 1–598. $7.00.—This splendid text has had a long and respectful lineage. The first edition, by Frederic T. Lewis, was a free translation of Phillip Stöhr's Lehrbuch der Histologie. The third to fifth editions were rewritten by J. Lewis Bremer. Now Harold L. Weatherford carries on, bringing the material up-to-date and adding more than three hundred new figures, many in color. The two previous authors and other colleagues at Harvard aided Dr. Weatherford in the large task of revision. The result is a comprehensive, finely illustrated and well-documented treatment of normal human histology.

Conservation in the United States. Second Edition. By A. F. GUSTAFSON, C. H. GUISE, W. J. HAMILTON, JR., AND H. RIES. Ithaca, New York: Comstock Publishing Co., 1944: i–xi, 1–477, figs. 1–236. $4.00.—The Cornell text on conservation has been revised to align it with new conditions and to incorporate new practices. It is a well-rounded, authoritative treatise, clearly presented, neatly printed and embellished by many fine illustrations. The treatment of wildlife, including the fisheries, is more nearly adequate than it is in most books on conservation.

Talk About Wildlife For Hunters, Fishermen and Nature Lovers. By ROSS O. STEVENS. Raleigh, N. C. (privately published by author, North Carolina State College, Raleigh, N. C.), 1944: 1–229, frontisp., figs. 1–97. $3.50 (cloth), $2.25 (paper).—With particular emphasis on the organization and functioning of state conservation agencies, Professor Stevens talks about wildlife, illustrating his ideas with cartoons and photographs. There is still much need for the improvement of wildlife administration, and for the crusading spirit which the author repeatedly exhibits, but the transcendent importance of competent personnel is perhaps not fully appreciated. Research, education, and restoration are properly stressed as leading items in the reform of wildlife affairs.

Studies on the Pacific Pilchard or Sardine (Sardinops caerulea). By OSCAR E. SETTE and Others. U. S. Fish and Wildlife Service, Special Scientific Reports Nos. 19–24, 1943: 173

pp., 2 pls., 49 figs. Processed.—These reports have a significance that may be partially lost because of the place and method of publication. They deal with the design of a research progam in conservation; problems of age and growth; the relation of temperature to the rate of development of eggs; methods of analyzing the size of natural populations, particularly of computing mortalities and replacements; and the distribution of eggs and larvae in reference to temperature and light.

Smoky Ridge. By FREDERIC DOYLE. New York and Toronto: Longmans, Green and Co., 1944: i–vii, 1–128, 10 pls. $2.25.—In simple and charming style, individualizing but not personifying the characters, the author of this little book presents chapters in the drama of animal life along the Smoky Ridge. The basic natural history is essentially sound, though a few general misconceptions are repeated, as when the black bear scoops a fish out of a stream and onto the bank with a swing of its paw.

AMERICAN SOCIETY OF NATURALISTS

THE new officers of the American Society of Naturalists, elected by mail ballot in place of the annual meeting which would have been held in December, 1943, are: *President,* Dr. FAY COOPER COLE (Anthropology), University of Chicago; *Vice-President,* Dr. CHARLES W. METZ (Zoology), University of Pennsylvania; *Secretary,* Dr. WM. RANDOLPH TAYLOR (Botany), University of Michigan; *Treasurer,* Dr. M. R. IRWIN (Genetics), University of Wisconsin (continuing); *Editorial Board,* THE AMERICAN NATURALIST, Dr. LEON J. COLE, Dr. A. FRANKLIN SHULL and Dr. LAURENCE H. SNYDER.

The society will meet with the American Association for the Advancement of Science in Cleveland, September 12–14, 1944. It is planned to hold the Biologists' Smoker on the evening of September 12, a Symposium and Business Meeting, probably on the afternoon of the 13th, and the Annual Dinner and Presidential Address on the evening of the 14th. The official headquarters for the society will be the Hotel Statler.

WM. RANDOLPH TAYLOR

THE CHARLES BENEDICT DAVENPORT MEMORIAL FUND

DR. CHARLES B. DAVENPORT, whose death occurred on February 18 of this year, had served from 1898 until 1923 as director of the

Biological Laboratory, and from then until his death as secretary of the Long Island Biological Association. At a meeting of the Executive Committee of the Board of Directors, in the latter part of February, a resolution was passed expressing a sense of irreparable loss in the death of Dr. Davenport, who, to a greater extent than any other individual, was the founder of the Biological Laboratory. Among all his fellow workers and neighbors his memory will stand not only for high attainment but also for an abiding example of integrity, helpfulness and warmth of heart. The Executive Committee decided at that meeting to ask the members of the association, as well as friends and colleagues of Dr. Davenport, to contribute toward the establishment of a fund in his memory, the interest of which should be used for aiding scientific research in the biological field. Checks or other contributions in the form of government bonds or securities for the Charles Benedict Davenport Memorial Fund should be made payable to the Long Island Biological Association, and addressed to the Biological Laboratory, Cold Spring Harbor, New York, or to Mr. Marshall Field, Treasurer, Huntington, New York. Contributions made to this fund are deductible for income tax purposes.

SHORTER ARTICLES AND DISCUSSION

HETEROCHROMOSOME FORMATION IN THE GENUS *ILEX*

During an investigation of some American species of the genus Ilex, several interesting phenomena were studied among the meiotic chromosomes in microsporogenesis. The sexual habit of this genus is not stable, even though many forms are functionally dioecious. Polygamous specimens and individual trees which change from female to perfect to female types during and immediately following transplanting are not uncommon. It is a moderately large genus—Engler and Diels set it at 280 species limited mostly to the American hemisphere—and contains both evergreen and less familiar deciduous varieties. Since the genus is obviously evolving toward a strictly unisexual condition and is represented by about 20 species in the eastern United States, some of which are certainly quite closely related, two evolutionary trends appear to be present in the same genus, namely, a trend from perfect to the dioecious state and the trend of recent interspecific hybridization. A study of the interplay of two such trends gave promise of results. The observations to date are encouraging, and this initial investigation may stimulate further work by cytologists to whom material of the great majority of species in this genus is readily accessible in North and South America.

A number of plants from each of five species of Ilex were studied and in all these some meiotic abnormalities were discovered during microsporogenesis. In some respects these peculiar chromosomes display characteristics frequently associated with the conventional conception of sex chromosomes, and yet other criteria of sex chromosomes are absent. Therefore the term *heterochromosome* will be used with the connotation that such chromosomes as deviate either from the behavior of the remainder in the complement or from the structure or behavior, or both, of its synaptic mate are called heterochromosomes. The anomalies found in each species are summarized as follows:

Ilex decidua Walt. (n—20). Some precocious chromosomes and occasional anaphase bridging during the heterotypic division. Lagging of several chromosomes and ejection of one anaphase chromatid during second meiotic division in about 50 per cent. of PMCs. No extruded chromatin survived into microspore formation. Evidence of heterochromosomes present.

I. monticola Gray (n—20). Slight lagging during late anaphase of first meiotic division with one chromatid of smallest chromosome consistently ejected into cytoplasm just prior to telophase of first division. Ejected chromatid attempts precocious second division, which does not succeed. In about half of the PMCs, the ejected chromosome is left out of the daughter nuclei and degenerates in the cytoplasm at conclusion of the regular second meiotic division. Heterochromosome in this instance is the smallest member of the complement.

I. opaca Ait (n—18). A medium-sized chromosome is precocious as to division but laggard in migratory ability and often remains at the equatorial plate at the conclusion of the heterotypic division. It undergoes no further division during the second meiotic division and is left to degenerate in the cytoplasm of about 50 per cent. of the PMCs. Frequently half of this heterochromosome is accepted by one of the daughter nuclear groups.

I. verticillata (L.) Gray (n—18). There is one very small chromosome in this species which appears to be tripartite, $X—Y_1–Y_2$, with one terminal section larger than both the smaller units together. This chromosome is often ejected into the cytoplasm as is one chromatid of a medium-sized pair and degenerates during first telophase, which is unlike behavior in other species. These unusual events were found in about half the PMCs, meiosis in the remainder being quite normal in every visible respect.

I. vomitoria Ait (n—20). The single minute chromosome in this species is normal and no ejected chromatin was found in any PMCs. A tripartite complex appears during heterotypic metaphase, but the chromosomes are too small to follow the history of this complex with any degree of accuracy. The complex is laggard during both metaphase and anaphase, almost completing an anaphase bridge, and in some instances indicated a 2–1 separation.

There is no evident uniformity in meiotic behavior among the five species investigated. The chromosome number is aneuploid, but 20 might prove to be the common haploid number since four larger chromosomes were quite often associated during the heterotypic metaphase and may indicate that originally the basic number was five. The pollen in all the species investigated appears to be structurally perfect, although there seemed to be a difference in the rate of maturity as demonstrated by some anthersacs wherein approximately half the microspores contained a dense cytoplasm which took a deeper stain than the remaining spores.

The presence of lagging or precocious chromosomes, occasional anaphase bridging of chromosome complexes, the ejection of chromatin from the spindle and its presence in the cytoplasm during telophase, the resulting variation in chromosome complements of the microspores, all such phenomena are reminiscent of meiosis in plants of hybrid origin. Although the abnormalities in the case of these five species of Ilex are not so violent as to jeopardize the fertility of the plants, yet they indicate that interspecific hybridization has extended through the eastern North American species in the past and has undoubtedly contributed to the multiplication of species. The presence of active hybridization in relation to the trend towards unisexuality in the genus Ilex may be better understood when compared with the situation found in a genus such as Thalictrum, which contains both perfect, polygamous and strictly dioecious types. The genus Thalictrum is vastly polyploid, with haploid numbers ranging from 7 to 70. The distribution of these numbers includes species with both high and low numbers native to all continents in the northern hemisphere and no distinction can be made between the perfect and dioecious types on the basis of chromosome number. The author wishes to add several new numbers to the array for which Langlet and Kuhn are largely responsible. Meiosis is quite normal in these species: as determined from collections made in Buncombe and Madison counties in western North Carolina.

Thalictrum clavatum	n— 7
Th. dioicum	n—14
Th. polygamum	n—42
Th. coriaceum	n—70

The extensive polyploidy accompanied by regular meiosis, so well displayed by the species of Thalictrum, is generally conceded by cytologists to be the consequence of previous hybridization. However, in this genus it is obvious that polyploidy occurred before the genus moved from the hermaphroditic habit since unisexual as well as perfect types possess the basic number of 7 as well as many of the higher haploid numbers. In other words, unisexuality has not affected the meiotic process at all. The situation is markedly different among the species of Rumex where in the hermaphroditic Eulapathum section there is vast polyploidy and normal meiosis in contrast to the dioecious Acetosa section where aneuploidy is accompanied by irregular meiosis. Thus we may conclude that in the case of Thalictrum interspecific hybridization came first and then the later advent of the unisexual state in some species. Although the evidence is still fragmentary, the situation is otherwise in Ilex. Here the chromosome evolution has been held to a very limited aneuploidy and in recent times probably a negative evolution through the loss of chromatin. Because each act of fertilization also becomes an act of hybridization in dioecious heterozygous types, meiotic abnormalities appear to be able to persist over a period of many generations. Although there probably is no uniform quantity of time required for the evolution of the unisexual habit, the absence of strictly perfect species in Ilex suggests that the dioecious condition is much older in species of Ilex than in Thalictrum. One might therefore conclude that the occurrence of heterochromosomes in Ilex lies in the unique combination of hybridization and the advent of unisexuality at approximately the same time in the phylogeny of the race. Investigators who seek the origin of sex chromosomes among higher plants are limited to phenomena akin to such as are found in the five species of Ilex as the only general and natural source of meiotic disturbance capable of providing the mechanism and the ability to survive through many generations. Laboratory treatment of specimens in order to produce similar vagaries lacks the asset of pertinency possessed by natural types which display these anomalies. The heterochromosomes described for species of Ilex are not sex chromosomes. However, they do supply intermediate steps between autosomes and the X–Y or X—Y_1–Y_2 types and provide us with a rational basis for further investigation on a host of plants which, like species of Ilex, have been subject to both previous hybridization and a change of sexual habit.

The question of survival of these meiotic irregularities through several generations and their adoption as a general characteristic of the species presents an interesting point for speculation, particularly in regard to the presence of heterochromosomes in species of Ilex. As with so many other biological problems involving inheritance, two alternatives offer themselves and our choice will certainly affect our subsequent point of view on details of chromosome evolution. On the one hand we may conceive of a unique meiotic irregularity (a heterochromosome, for example) occurring in one set of chromosomes somewhere in the sporogenous tissue of one plant of a given species. This unusual chromosome must impart two attributes to the offspring of the plant in which the heterochromosome has been incorporated through a previous successful fertilization. First of all, it must impart the ability to insure the survival of this heterochromosome through successive reduction divisions. It must also impart to the offspring a competitive advantage over neighboring members of the same species so that the offspring of the neighbors are gradually eliminated from the main line of descent for the race while the offspring of the heterochromosome bearing plant gradually usurp the earth afforded the species.

On the other hand, we may conceive of general trends such as hybridization and the assumption of the unisexual habit as forces which affect great numbers of a given population more or less simultaneously over a wide ecological area. These forces would cause unique chromosome mechanisms to arise in many individuals and because of their common distribution within a given species and their similar evolutionary direction they would be able to survive on a broad front. With this conception the necessity for a competitive advantage accruing to the individuals possessing the heterochromosome is not nearly as exacting as in the first hypothesis. The first alternative appeals to the cytogeneticist because it offers a neat mechanism which can be tested under laboratory conditions and appears to be parsimonious with broad assumptions. The second, however, appeals to the ecologist, the systematist, the comparative anatomist who seeks an explanation of things as they grow in the fields in profusion and are scattered around the earth. Perhaps this is another facet of the macro-micro-evolutionary dispute. This is not the place to elaborate the issue, but merely indicate that in the case of the five species of Ilex the meiotic abnormalities would tend to diminish the chromosome number, which does not appear to be the case. This suggests that the nuclei which effect fertilization come from microspores which have the full complement, the half of the PMCs which were regular in meiosis. Yet the ability to disturb the meiotic process sufficiently to produce the heterochromosomes must then be passed on through either the PMCs which do not display it or through the female side. In either event we have a possible means of carrying a meiotic peculiarity from one generation to the next without materially affecting the fertility of the individuals and yet affording a unique chromosome complex out of which so-called sex chromosomes might eventually arise.

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A RELATION BETWEEN CHROMOSOME SIZE AND B VITAMIN CONTENT OF RAT ORGANS

THIS preliminary report deals with a chromosomal differentiation of rat organs that is apparently concerned quantitatively with B vitamin concentration, probably through the mediation of enzymes produced by the chromosomes.

It has been conjectured that enzymes or their specific active groups are exact replicas of genes (Wright, 1942). Antigens are produced under the influence of one or a few genes (Irwin and Cole, 1936; Irwin and Cumley, 1943), and their production has likewise been conceived as a modeling synthesis similar to that imagined to occur in the reproduction of genes (Haldane, 1937). Caspersson (1941) has come to the view that, while heterochromatin produces the histones and ribonucleic acid of the nucleolus, the euchromatin synthesizes ''higher'' proteins.

Recently the isolated nuclei of rat liver have been shown to contain a number of enzymes. Dounce (1943) has demonstrated arginase, cytochrome oxidase, esterase, lactic acid dehydrogenase, alkaline phosphatase and acid phosphatase, while Lan (1944) has found *d*-amino acid oxidase, uricase and choline oxidase in isolated nuclei in activities approaching their activities in whole liver. The finding of Isbell, Mitchell, Taylor and Williams (1942) that in isolated nuclei of beef heart and of mouse cancer there are appreciable quantities of the B vitamins suggests the presence intranuclearly of enzymes that contain these vitamins within their prosthetic groups.

It is therefore of interest that the size of chromosomes in various normal rat organs should be closely paralleled by the total concentration of the B vitamins, thiamin, riboflavin, nicotinic acid, pantothenic acid, pyridoxin, biotin and folic acid. From acetocarmine preparations made according to the method of Painter (1939) 25 metaphase figures in each of a number of rat organs were drawn under oil immersion with a camera lucida. The drawing magnification was 3,000. The average volume of chromosome per metaphase was calculated by a method previously described (Biesele, Poyner and Painter, 1942). The average chromosome volumes given below are for organs of an 84-day-old male Wistar rat, with the exception of the adrenal gland, that was taken from an adult male Osborne-Mendel rat in which the liver and kidney chromosomes agreed in volume with those of the adult Wistar rat. It was found that the organs were arranged in this order according to approximate average chromosome volumes: liver, 1.1 cubic micron; kidney, 0.9 cubic micron; adrenal, 0.7 cubic micron; and lung, small intestine, and spleen, 0.5 cubic micron. Correspondingly, the organs of the adult Wistar rat have the following arrangement in descending order of arbitrary units of total B vitamin concentration: liver, 10; kidney, 6; adrenal, 5; spleen, 3; and lung, 2, according to data given by Mitchell and Isbell (1942), and Taylor, Pollack and Williams (1942). These authors did not assay the small intestine. Inositol was omitted from the calculations of total B vitamin concentration because it seems to be concerned more in phospholipid structure than in enzyme systems (Bollman, 1943). The actual mean values of the average chromosome volumes determined, together with their standard deviations, are spleen, 0.46 ± 0.10; small intestine, 0.50 ± 0.12; lung, 0.51 ± 0.11; adrenal, 0.72 ± 0.13; kidney, 0.93 ± 0.26; and liver, 1.12 ± 0.31 cubic micron. Although the first three values are not significantly different statistically, every other possible pair differs significantly except for the kidney and liver, in which, however, the difference between the means is between 2 and 3 times its standard deviation. There is a statistically significant difference, furthermore, between 1.02 ± 0.27 cubic micron, the mean of the average chromosome volumes of 237 metaphases of the livers of 7 adult male rats, and 0.89 ± 0.21 cubic micron, the mean of the average chromosome volumes of 50 metaphase figures of the kidneys of 2 adult male rats.

Embryonic rat liver has about half the B vitamin concentration of adult liver (Williams, Taylor and Cheldelin, 1941), and the activities of a number of its enzyme systems are considerably lower than those of adult liver (Greenstein and Thompson, 1943). Correspondingly, the liver chromosomes of a newborn male Wistar rat were found to average 0.72 ± 0.16 cubic micron instead of 1.12 ± 0.31 cubic micron as in the liver of the older rat. Chromosomes have the same range and frequency of sizes in regenerating and control livers of the rat (Biesele, 1944), and according to Greenstein and Thompson (1943) enzyme activities in regenerating livers are in good agreement with those in normal adult rat livers.

Perhaps the best interpretation to give at present to the direct relation between average chromosome volume and B vitamin concentration in rat organs is that the development of the chromosomes, as seen in metaphase of mitosis, is an indication of the total synthetic activity of the chromosomes in producing protein apoenzymes that combine with vitamins and thus determine the bound vitamin capacity of the organ. While the probable importance of cytoplasmic synthesis of proteins and enzymes is not to be denied, it is desired to emphasize that differentiation of the cell may proceed in part through differential synthetic activity of the chromosomes and genes.

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OVARIAN ACTIVITY OF *XENOPUS LAEVIS* WHILE IN CAPTIVITY[1]

Owing to the recent widespread clinical use of *Xenopus laevis* (South African clawed frog) in human pregnancy diagnosis, many reports have been forthcoming regarding the physiology of ovulation in this unusual amphibian. In the test for pregnancy, *Xenopus laevis* extrudes ova within six to twelve hours following injection of urine containing gonadotropic hormones characteristic of pregnancy.

It was at first thought that captivity caused atrophy and involution of *Xenopus laevis* ovaries. Numerous investigators have since shown that ovarian activity continues in captivity, provided, however, that optimum conditions with regard to food, environment and housing are maintained. Aronson (1944) in a recent paper seems to doubt the continued activity of *Xenopus laevis* in captivity, stating that "there is no reason to believe that these toads (*Xenopus laevis*) constantly ovulate." He offers no concrete evidence to support his statement except the work of Berk (1939), who found a seasonal variation in ratio of the weight of the gonads to the body weight of *Xenopus laevis*. Berk, on the other hand, studied these animals in their natural habitat in South Africa.

Having studied these frogs in captivity over a period of five years, our findings consistently agree with the accepted belief that ovarian activity in *Xenopus laevis* continues throughout the year (Weisman and Coates, 1944). The following experiments will show that ovulation in *Xenopus laevis* is unquestionably continuous while in captivity.

Experimental Part

Studies with injections of chorionic gonadotropic hormones: Over a period of four years we have constantly injected *Xenopus laevis* with crude extracts of the urine of pregnant women. Two thousand frogs were so treated during 48 consecutive months. Of these animals, 98.9 per cent. reacted within six to eighteen hours by extrusion of hundreds of mature ova. The remaining few non-reacting animals were injected a second time with more potent extracts, and in each instance a positive egg-extrusion reaction was noted. In other words, if the dosage of the hormone is sufficiently high no healthy female *Xenopus laevis* ever failed to extrude ova following such gonad stimulation.

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Studies of ovaries of animals autopsied: During the course of our research 38 frogs died instantly from either a technical error in injection or a toxic hormone concentration. These animals were all autopsied and studied for gonadal activity. All the frogs were found to contain thousands of ova in various stages of maturation. The autopsies were performed whenever the animals chanced to die and the records of our autopsies indicate that at least one dead animal was studied each month. We have never found *Xenopus* ovaries atrophic or anovulatory.

DISCUSSION

From the preceding experiments, it is at once evident that *Xenopus laevis* differs from *Rana pipiens* and other common American frogs. Regardless of the season of the year, *Xenopus laevis* can be said to be constantly ovulating as shown by its consistent rapid egg-extrusion response and the state of the ovaries at autopsy. *Rana pipiens,* on the other hand, does not respond to gonadotropic activity except during its normal egg-laying period and then only to tremendous doses of gonadotropic stimulation.

SUMMARY

Two thousand *Xenopus laevis* were injected with extracts of chorionic gonadotropic hormones. In every instance, and regardless of the season of the year, egg-extrusion followed potent hormone stimulation within six to eighteen hours.

Thirty-eight animals were autopsied and the ovaries studied for gonadal activity. Each animal showed definite evidence of continuous ovarian maturation and activity.

Regardless of the time of year, *Xenopus laevis* constantly carries ovaries filled with ova in various stages of maturation. Hundreds of these ova are brought to full maturity within six to eighteen hours following artificial gonadotropic hormone stimulation.

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THE
AMERICAN NATURALIST

VOL. LXXVIII *September–October, 1944* No. 778

NEW LIGHT ON EVOLUTION FROM RESEARCH ON THE GENUS CREPIS[1]

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THE theory of organic evolution is now generally accepted by enlightened people. They think of the many kinds of plants and animals which inhabit the earth as having descended from very different ancestors. Botanists believe that all our flowering plants have evolved from simpler forms in which the sexual organs were produced on some vegetative part of the plant. And these flowerless plants are believed to have descended from still simpler forms. The account of animal evolution is in general similar. More complex or more specialized forms have evolved from less complex or less specialized forms. What are the general principles underlying this grand process of organic evolution?

The concept that the many different species of living things now inhabitating the earth have all descended from earlier species, and those from still earlier species, and so on back to the origin of life on the earth is the primary thesis of the theory. This concept is based on two general principles: (1) the continuity of physical life which is made possible in higher plants and animals by sexual reproduction; and (2) the metamorphosis of species—new species arise from pre-existing species.

This second principle was the basis of Charles Darwin's classical theory. Darwin assumed that the evolutionary process, which he termed "descent with modification,'' was made possible by the gradual accumulation of small changes under the influence of natural selection. And natural selection was assumed to operate through the preservation of those individual organisms which were able either to live in a changing environment or to escape from it into a new region where the environment is favorable. In spite of all doubts and attempts to disprove it in the past, this principle of natural selection is recognized to-day as an important factor in organic evolution. But it is only one of several factors. Another is the way or ways by which the individuals comprising a species reproduce themselves; because this too affects the preservation of such new hereditary changes as may occur from time to time. Also of importance is the number of individuals making up the population (or populations) of a species, at least when the number is below a certain optimum. For, in inverse proportion to the population size, there is random elimination of hereditary elements in each generation, because these hereditary elements or genes are shuffled about among the germ cells, and many more germ cells are formed than can function in producing the individuals of the next generation. This in itself tends to produce changes in species.

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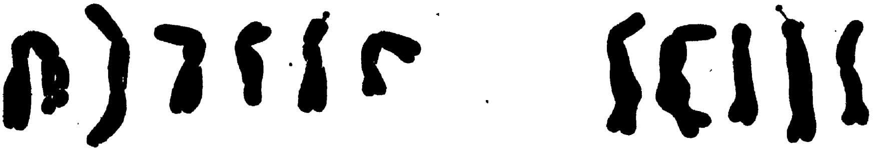
[1] The Faculty Research Lecture for 1944 at the University of California, Berkeley (revised for publication).

But all these so-called factors are merely the conditions which determine the preservation of genetic changes in the species. The more basic problem, which was sensed but not solved by Darwin, is to discover the real nature of those hereditary changes which are continually occurring in individuals and which, under favorable conditions, may make possible a new character or quality of the species. Two things, however, Darwin did stress: first, that these changes in individuals, which lead eventually to the origin of new species, are probably small; and second, that modification by descent is a slow, gradual process.

Just the opposite conception, to wit, that new species result from a single drastic change, affecting many parts and functions of the organism, has had its advocates among biologists, beginning with de Vries in 1901. Very recently this theory has been revived by one of our colleagues on the grounds that true species differ from one another in some more subtle yet profound way than do mere subspecies or varieties; and that new species originate through some sort of "systemic mutation," due perhaps to the alteration of the chromosomes. However, the opposite view, namely, that the differences between species and subspecies are largely matters of degree of differentiation, is accepted by the majority of biologists. And Darwin's original view, that species change gradually into new species through the slow accumulation of small changes, is the prevailing view to-day. The evidence from *Crepis* certainly supports this view, as I shall try to show. But first we need more definite ideas about the nature of those genetic changes which may gradually bring about the transformation of one species into another.

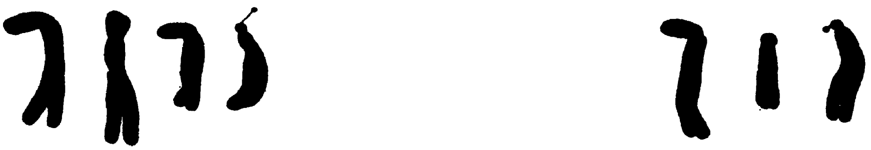
I shall introduce these ideas while introducing you to the group of plants on which I have been working for the past quarter-century. *Crepis* is a large genus, containing 196 species. Only one of these species, the pink-flowered *Crepis rubra,* has become a common garden flower. All the others are wild species, a few of them being weeds. As a group, *Crepis* is closely related to *Lactuca,* which contains the lettuce of our victory gardens, and to *Taraxacum,* which includes the common dandelion and its wild relatives. After bringing together the dried specimens of all these *Crepis* species from various herbaria, I was much impressed by the extraordinary diversity within the group with respect to the size and habit of the plants as well as the form of their roots, leaves, flower heads, and especially their fruits or so-called seeds. These plants, it seemed, must also exhibit great diversity in their life processes, since the various species are peculiarly adapted to extremely different environments, such as swamps, deserts, meadows, seashores and alpine peaks.

In course of time I was able to obtain live seeds or roots of many species of *Crepis;* and this enabled us to make our microscopic studies of their chromosomes. Eventually it was found that most of the species have either 8, 10 or 12 chromosomes in their somatic cells; but three species are known which have only 6. In Fig. 1 are shown camera lucida drawings of one member of each pair of chromosomes found in root tip cells from: *Crepis terglouensis,* a high alpine perennial known only from the European Alps; *Crepis pontana,* another alpine perennial of the European Alps; *Crepis tectorum,* a widespread annual of Asia and Europe; and *Crepis capillaris,* a widespread European annual which has become established as a lawn weed here and there in North America, New Zealand and probably other parts of the world.



C. terglouensis

C. pontana



C. tectorum

C. capillaris

Fig. 1

Now the chromosomes are found in each of the thousands of tiny cells of which the plant or animal body is composed; they usually exist in pairs and they contain the all-important hereditary elements or genes. A single chromosome may contain hundreds of genes; and since a complete set of genes is essential to normal growth and development, each individual has the same number of chromosome pairs in all its somatic cells. But, when the germ cells are formed, each cell gets only one member of each pair of chromosomes. Thus each germ cell has one complete set of genes, whereas the fertilized egg and all the body cells contain two doses of each gene, one from each parent.

Up to the present it has been possible to study the chromosomes in 113 species of *Crepis*. Since most of the species have either 12, 10, 8 or 6 chromosomes, that is, 6, 5, 4 or 3 chromosomes in their germ cells, the question arises as to how such a basic series was created. If this could be discovered, it might also be possible to learn whether a change in chromosome number causes changes in form, structure or function in the plant, or in other words, whether the changes in chromosome number which occurred during the evolution of these *Crepis* species have any causal relation to the changes in the morphology and physiology of the plants. Since the changes in chromosome number, which created the series, 6, 5, 4, 3, must involve the loss or addition of a single chromosome from the basic set, it would appear that such changes might be merely mechanical in nature. Does the origin of new species depend primarily upon such changes in chromosome number or upon some more fundamental type of genetic change such as gene mutation?

And what, you may ask, is gene mutation? Also if genes change how does one account for hereditary resemblance and the stability of many species? The answer to the second question is that genes are actually stable entities and yet they are so constructed as to be capable of an occasional change. To express one's concept of gene mutation one must first have a concept of a gene.

A gene may be thought of as a molecule or part of a molecule and a gene mutation as a molecular change of some sort at a definite point in a particular chromosome. The chromosomes are known to contain organic molecules so complex in structure that the number of possible per-mutations and combinations of changes by loss, addition or substitution of small groups of atoms at different points is well-nigh infinite. Hence it is conceivable that, sooner or later, any gene may undergo a change. And, since there are hundreds of genes in one set of chromosomes, and thousands of germ cells each with that same set of chromosomes, there would seem to be a good chance that some single gene in some particular germ cell might mutate. As a matter of fact geneticists have learned by experiments that gene mutations actually do occur at different rates in different genes and under different conditions. Some genes change rarely, others more frequently, and still others very frequently under comparable conditions.

Now gene mutations are recognized by some geneticists as being of two general categories which may be designated as major or primary and minor or modifying, though the distinction can not be clear-cut, because some mutations are border-line cases. It should be emphasized that what we are actually describing when we use these terms, major and minor, or primary and modifying, is the observed effects of the gene change, not the gene itself.

A major gene change so influences the development of the individual as to cause easily observable changes, either morphological or physiological or both. These changes range from differences in size, shape or function of parts up to monstrosities or even to lethal effects. For example, in *Crepis tectorum* some perfectly normal plants possess an interspecific lethal gene in double dose. When such a plant is crossed with another species, *Crepis capillaris,* plenty of hybrid seeds are produced but all the young seedlings die. Other *tectorum* plants have one lethal gene and one normal partner of that gene. Such a plant, crossed with *C. capillaris,* produces plenty of seedlings but half of them will die. Still other *tectorum* plants have the two normal partners of the lethal gene, and their offspring from crossing with *C. capillaris* will all live and will develop and produce flowers. Thus the gene-mutation that produced this interspecific lethal is clearly a major change.

In another species, *Crepis foetida*, there exists a gene difference which affects only the shape of the juvenile leaves. After the plants develop beyond the early rosette stage their juvenile leaves disappear and they can not be classified according to the character mentioned. Now the mutation which caused this gene difference is really on the border line between the major and minor categories.

The strictly minor mutations actually cause such small changes that they can be detected with difficulty if at all. And yet, by careful selection experiments, like Castle's famous research with modifying genes in hooded rats and Whiting's recent discovery of modifying genes affecting sex in a parasitic wasp, it has been shown that these minor genes operate together in series and thereby profoundly affect adult characteristics. One such minor mutation may not be notable to an observer, but when it has been recombined with other genes or with more modifiers of a similar nature, the results will provide material for the effective operation of selection. Thus it is possible for a species population to undergo a gradual change in its characteristics through the birth of certain individuals which possess new minor mutations. Furthermore, the combined effects of fortunate combinations of genes may gradually bring about important changes in some part of the species population. It only remains for this changed segment of the population to become separated from the rest through migration or by possible environmental change or by some internal change within the plant, making reproduction with the original type of the species impossible, to have the stage set for the origin of a new species.

One may ask, therefore, what have been the roles played by gene mutations on one hand, and by changes in chromosome number on the other hand, in organic evolution?

To this fundamental question the research on *Crepis* has revealed some definite answers which I shall present toward the close of the lecture.

Before reaching the vantage point from which such generalizations could be made, it was necessary to arrange the species of *Crepis* in sections such that the members of each subgroup are more closely related to one another than to the members of any other section. In classifying the species into subgroups, my constant aim has been to arrange both the sections and the species in each section in their probable phylogenetic sequence. By this is meant an arrangement representing, as nearly as possible in a linear series, an orderly progression from the oldest or most primitive species to the youngest or most advanced species. At this point let me anticipate the presentation of the evidence to say, this evidence will show that there is an actual difference, and a great difference too, in the comparative length of time that the most primitive and most advanced species have been in existence. Therefore, we are actually warranted in calling them the oldest and youngest species in the genus. In other words, no matter how different the youngest species may look from the oldest ones in the series, our evidence shows that they have descended from those oldest species, or similar ones that are now extinct, through a long line of interconnecting forms.

The hazards of phylogenetic speculation are well known to biologists. But most such speculations in the past have been based largely on evidence obtained from a single biological discipline—most often from morphology alone, or from morphology supplemented by anatomy. For this reason I have based my phylogenetic classification on as broad a foundation as possible by obtaining and synthesizing evidence from several different disciplines, all for the purpose of determining the true relationships between the species. Although my first classification was made on the basis of morphology, it has been checked and rechecked against the evidence from the chromosomes, from experiments with hybrids, from geographic distribution and from any other evidence available.

The morphological criteria of phyletic relationship need not be discussed in detail here. Briefly, it was found that the most primitive species in the genera are robust, leafy perennials with few large flower heads in which the involucre consists of many large scales or bracts that remain unchanged as the fruits ripen. The individual florets and fruits or achenes are also comparatively large; and the achenes are not highly specialized for distribution of the seeds by the wind. In marked contrast, the most advanced species are slender annuals with a basal rosette of leaves and nearly naked stems, numerous very small flower heads in which the involucre consists of a few small bracts that become thickened and reflexed as the fruits ripen. The individual florets and fruits or achenes are very small; and the achenes are highly specialized for wind distribution by the presence of a long slender beak which bears the fine pappus bristles like a parachute at its summit. All the other species in the genus fall into subgroups which form a connecting series between the two extremes.

The chromosomes have provided some valuable evidence on phyletic relations in *Crepis*. When we compare the karyotypes with longest and shortest chromosomes in each of the four number classes, 6, 5, 4, 3, we find that we have selected a more primitive and a more advanced species in each case. There is in fact a definite tendency in this genus for the younger species to have shorter chromosomes. There is also a tendency for the chromosomes to be more asymmetrical in the more advanced species. These are interesting trends, but they are merely coincidental. The most important phenomenon for the present discussion is the progressive reduction in chromosome number from 6 to 5 to 4 to 3, since the majority of the species in the genus belong in this series. I might add that there are a few species of *Crepis* with other chromosome numbers. For example, there is one section having the germ cell number 7 and one in which it is 11 or some multiple of 11. But these are subsidiary groups with special problems as to their origin. They are side issues from the main line of events in the evolution of the genus.

Statistical analysis has revealed two very important trends in the evolution of this genus. (1) There is strong positive correlation between phylogenetic position and chromosome numbers. On morphological grounds, sections I—V contain the most primitive species in the genus and the majority of these species have 6 chromosomes in their germ cells. On the same basis sections XIX—XXVII contain the most advanced species in the genus and the great majority of these have 4 or 3 chromosomes in their germ cells. In the intermediate sections the chromosome numbers are about equally divided between 5 and 4. (2) There is also strong positive correlation between phylogenetic position and length of life of the individual plant. In the primitive sections the plants are all perennials; in the most advanced sections they are mostly annuals, and the most advanced species are the shortest lived of all the annuals. Thus it is clear that reduction in chromosome number and shortening of the life cycle have both gone along with morphological reduction and specialization. And we are assured of consistency in the phyletic evidence from the first three fields, morphology, physiology and cytology.

Now the evidence from genetics and cytogenetics is also consistent with all the other evidence. The interspecific lethal in *Crepis tectorum,* illustrates a major gene difference; and the two types of juvenile leaves in *Crepis foetida* were mentioned as a borderline case approaching the minor category of gene differences. In several of our artificial crosses between species having the same chromosome number, we have obtained data showing that the two species differ in numerous minor gene differences affecting the size and shape of various parts of the plant.

From this we infer that these species have diverged from a common ancestor through the accumulation of minor gene mutations. This is one important contribution from the genetic studies.

Another contribution from genetic research is found by summarizing the results of 170 different crosses between *Crepis* species. The most significant thing about these data is the support they give to the arrangement of the species in their sections. These attempts to obtain artificial hybrids were made over a period of 25 years and the choice of parents was determined by the species available at the time. There are two types of crosses, intrasectional and intersectional. In the first type the species crossed were always in the same section and eight sections are represented in these experiments. In the second type the two species crossed were always in different sections and 17 of the 27 sections are represented in these experiments. There were 43 crosses of the first type and of these only 7 per cent. failed while 93 per cent. gave hybrids. Over 80 per cent. of these hybrids were vigorous plants and a third of these were fairly fertile also; whereas only 17 per cent. were weak and sterile. Of the second type, intersectional crosses, 127 were attempted, and of these 40 per cent. failed and only 60 per cent. produced hybrids. Of these hybrids only 60 per cent. were vigorous and none were fairly fertile, whereas all were nearly sterile and 40 per cent. were very weak plants. This evidence clearly indicates that the sections represented in these experimental crosses are groups of species that are more closely related to one another than to the species of other sections. To this extent it strongly supports the sectional scheme of classification which was worked out on a morphological basis.

Two contributions from cytogenetics will be presented because of their important bearing on organic evolution. The first is the work of a Russian worker. By treating seeds with x-rays, examining the chromosomes of the seedlings, and practising adequate breeding technique, Miss Gerassimova eventually obtained a plant of *Crepis tectorum* which still had all the chromosome material present and which looked just like the original plant. But pieces of the chromosomes had been interchanged between different pairs so that the new type, *Crepis nova* has two long V-shaped pairs and two very short pairs (note shape of chromosomes in normal *C. tectorum,* Fig. 1). This new chromosome type not only looks externally like other *tectorum* plants but it is equally fruitful when self pollinated. Yet, when it is crossed with the original, normal *tectorum* type, the hybrids are as highly sterile as the hybrids between many true species. Thus *Crepis nova* is sexually isolated from normal *tectorum* plants. And, as Miss Gerassimova points out, the sexual isolation of two parts of the same population makes possible their gradual differentiation by means of gene mutations. These may change an incipient species like *Crepis nova* more and more in size, shape and function of parts, even under similar environmental conditions, and at the same time, may increase its sexual isolation from its ancestor. Now the interchange of parts between different chromosome pairs was caused by the x-rays used in this experiment. But the same sort of mechanical changes also occur in nature. Though their cause or causes are as yet unknown, it is clear that such interchanges provide the first step in the reduction in chromosome number from 4 to 3, or 5 to 4, etc., as will be shown in the next contribution.

This is the research of Dr. Hassan Tobgy (1943), one of the Egyptian students who worked in our laboratories. He crossed *Crepis neglecta* with *C. fuliginosa* and made an intensive study of chromosome behavior in the hybrids. In Fig. 2, on the right is *C. neglecta,* and on the left *C. fuliginosa,* with reciprocal hybrids between, which look just alike. These hybrids were extremely sterile, producing almost no good seed, even though the two parent species are very closely related. This sterility of the hybrids is caused by the chromosome differences in the two species.

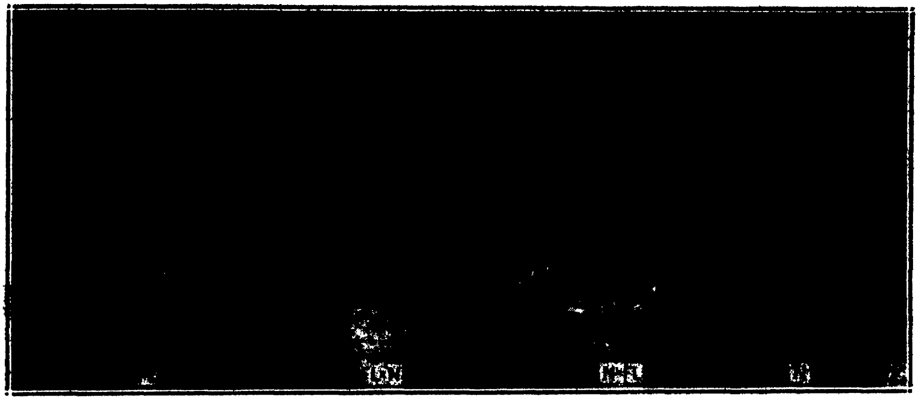


FIG. 2

In Fig. 3, at the upper left, are shown the 3 chromosomes in a germ cell of *Crepis fuliginosa,* labeled A_F, B_F, D_F. There are, of course, two A's, two B's and two D's in each somatic cell and in each spore mother cell. At the upper right are shown the 4 germ cell chromosomes of *Crepis neglecta,* A_N, B_N, C_N and D_N. You will note that the *neglecta* chromosomes are definitely wider than the *fuliginosa* chromosomes, so that in the hybrid set it is

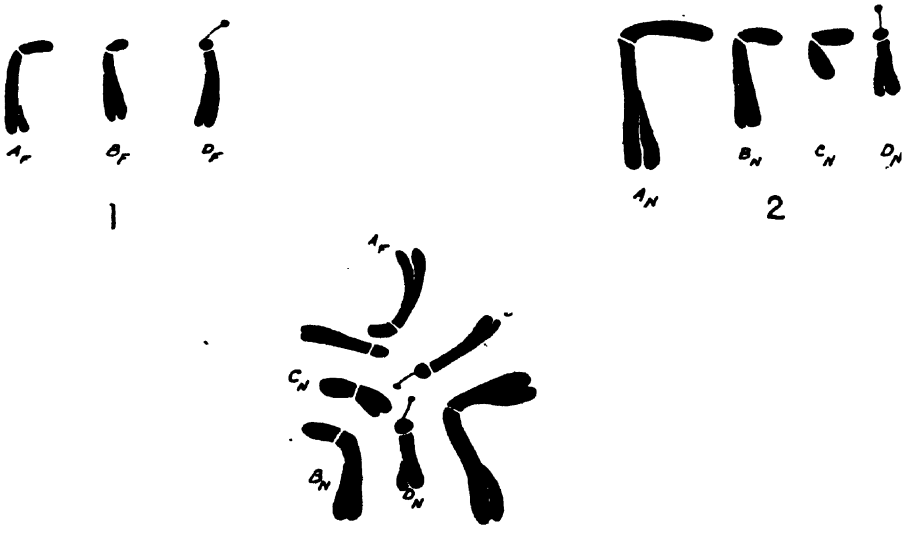


FIG. 3

easy to see that the 3 upper ones are the *fuliginosa* A, B and D and the others are the 4 *neglecta* chromosomes.

In *Crepis fuliginosa,* when a pollen mother cell is about to go through the reduction division, (Fig. 4, upper left) the two A chromosomes come together, also the two B's and the two D's, the latter being always associated with the nucleolus at this stage. Then (2) as the pollen mother cell (the surrounding wall of which is not shown) begins to divide, the 3 pairs of chromosomes orient themselves so that one A will go into one germ cell and the other A into another. Similarly with the two B's and the two D's. In the same way a pollen mother cell of *Crepis neglecta* has 4 pairs; and in the reduction division the members of each pair are separated into different cells (3, 4). Now let us compare these same stages in the hybrid. We find (5) a pair of A's, a pair of D's, and an association of three chromosomes, *neglecta* B, *fuliginosa* B, and *neglecta* C. Then, in division of the pollen mother cell (6), the two A's and the two D's are separated, while the B and C of *neglecta* are separated from the B of *fuliginosa.*

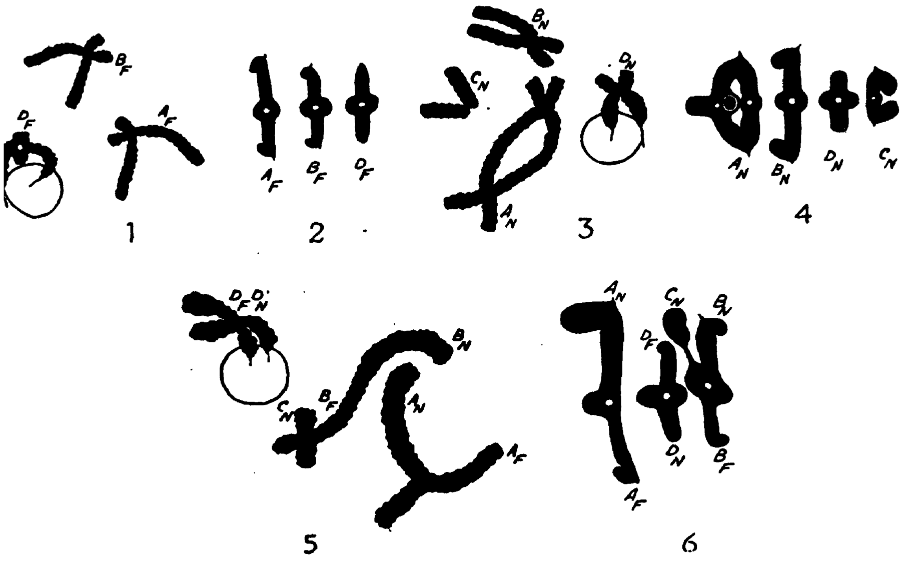


FIG. 4

From a great deal of evidence like this, but still more precise, Tobgy was able to show conclusively that the B chromosome of *Crepis fuliginosa* contains the essential hereditary elements of both the A and C chromosomes of *Crepis neglecta.* Therefore, the 3-chromosome species *fuliginosa* either originated directly from *neglecta,* or the two species arose from a common ancester, with 4 pairs of chromosomes. This cytogenetic evidence that a 3-chromosome species descended from a 4-chromosome species is of basic importance because it corroborates our other evidence on phylogeny in *Crepis.* Furthermore, we have similar evidence from the research of Marta Sherman Walters (1944) that a certain 4-chromosome species descended from a 5-chromosome ancestor.

We have examined some of the evidence on phylogeny in *Crepis* coming from comparative morphology, physiology, genetics and cytogenetics. Before attempting to describe the origin and development of this genus, it is necessary to consider the evidence from geographic distribution. All the evidence presented thus far agrees with the assumption that *Crepis* is monophyletic, that is, that the 196 species in this genus have descended from one ancestor, or from a small group of very closely related species, and therefore that there was one geographic center of origin. A study of geographic distribution aims to discover that center of origin and the principal migration routes followed in reaching the present world wide distribution of the genus.

The best evidence on center of origin is found by comparing the distribution of the older and younger species in each section. When this has been done it becomes clear that the distributional evidence from all the sections is consistent in pointing to north central Asia as the center of origin. A few sections will serve as illustrations.

In section 4, the older species are on opposite sides of Eurasia, three of them in the mountains of southern Europe, while the fourth is in northern Japan. The four younger species are nearer the assumed center of origin.

In section 6 all four species are primitive and they all occur in the Pyrenees, Alps and Balkan Mountains. But one of them, *C. conyzaefolia,* also has a disrupted distribution extending clear to the Altai Mountains, which is in the assumed center of origin. Hence this is a guiding species, having left behind some remnants marking its route of migration from north central Asia.

Section 12 contains seven species which are mostly in south central Asia. But *Crepis nana* also extends through the mountains of central Asia and Siberia into Alaska, arctic Canada, and south through the Rocky Mountains, and the Sierra Nevada. The seventh species, *Crepis elegans,* was obviously derived from *Crepis nana,* and it occurs only in North America. The distribution of this group is important in helping to establish the antiquity of *Crepis.* The center of origin for this section is evidently central Asia. Some at least of the isolated stations for *C. nana,* located in eastern North America, are on unglaciated islands in a heavily glaciated region. This certainly indicates that this species migrated from Asia into America before the Ice Age.

Section 21 is especially interesting. Two of the four species are in the Chinese-Tibetan Mountains. Another occurs in northeastern Siberia. The fourth, *Crepis multicaulis,* is most advanced and is a polymorphic species. It extends from the western Himalayas and Pamirs to the Altai; also it exists today on a small, probably unglaciated area in Varangar, the extreme northern end of Norway. Central Asia is surely indicated as the center of origin and it is probable that *C. multicaulis* was widespread in northern Europe before the Ice Age but was almost completely wiped out by Pleistocene glaciation.

Now we can safely generalize as follows: Assuming central Asia to be the center of origin for *Crepis,* we find general agreement in the geopraphic distribution of the various sections; and in certain sections we find striking conformity with a well-known principle of paleontology—Matthew's Principle—which states that, in groups of related species living at a given time, the most primitive will be found farthest from the center of origin. While numerous exceptions and modifications to this principle are known, it still holds generally for many groups of higher organisms. The conformity with Matthew's Principle which we find in *Crepis* strengthens our assumption that central Asia is the center of origin for this genus.

We can now turn our attention to the migrations of *Crepis* species away from the center of origin. But, in order to consider this problem intelligently, we must first consider the background of earth history and the antiquity of *Crepis.*

The background of earth history must be considered at least as far back as the Mesozoic era because it will be pertinent to inquire whether north central Asia has been continuously a continent since that era or even longer. If so, then not only *Crepis* and its immediate ancestors but its much more remote ancestors, extending back to the earliest forms of flowering plants and their ancestors, could have developed in that same region. This point will be mentioned again. As for the genus *Crepis,* we are concerned only with the Cenozoic era and, particularly in the Tertiary period, with the Miocene and Pliocene epochs; and in the Quaternary Period with the Pleistocene epoch which includes the Ice Age. The flowering plants as a group originated during the period preceding the Tertiary period. But, as we shall see, *Crepis* probably originated about the middle of the Tertiary period in early Miocene or late Oligocene.

Concerning the antiquity of *Crepis,* the distributional evidence alone is convincing. The map (Fig. 5) shows the present distribution of the genus. The numbers indicate sections. Without going into details, only three points need emphasis. (1) Sections 4 and 6 contain some of the oldest species in the genus and some of these are now found only at very high elevations in the European Alps.

These heights were covered with ice during the Pleistocene epoch; and European botanists agree that these alpine plants must have moved up onto the peaks from surrounding areas gradually as the ice disappeared. This means of course that they were already in that region at least as early as the Pliocene epoch. (2) The present occurrence of *Crepis nana* on small unglaciated areas in Newfoundland indicates that *Crepis* had a pre-Pleistocene origin; and the same reasoning applies to the isolated population of *Crepis multicaulis* in northern Norway. (3) Our study of the American species led

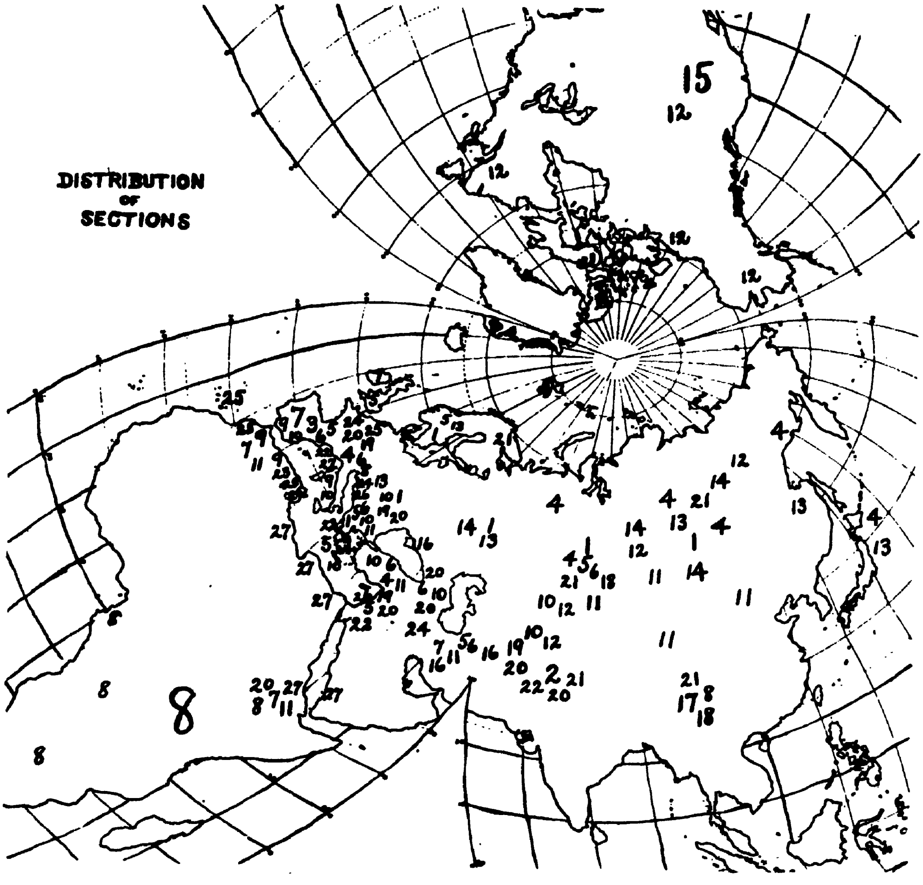


FIG. 5

Stebbins and myself (1938) to the conclusion that some of them or their ancestors must have migrated from Asia to America in the Miocene epoch.

The deductions from distributional evidence have been well substantiated by the discovery of some fossil seeds. These fossils were identified as three different species of *Crepis* by European botanists; and, from the excellent lithographs published by Reid and Reid (1916), I am satisfied as to their identity. In fact they are easily matched with seeds of the following present day species: *Crepis terglouensis,* a primitive relic species of the high Alps, having 12 chromosomes; *C. mollis,* another 12-chromosome species, but less primitive than the preceding and more wide spread; and *C. conyzaefolia,* the most primitive of all the 8-chromosome species. The last is the guiding species mentioned earlier. These fossils were found in Middle Pliocene clay pits, the Reuver plant beds on the Dutch-German border. In Tertiary times this area was in the huge delta of the Rhine River, which must have transported the seeds from the uplands. The point to be emphasized here is this: If these plants had already migrated from Central Asia, an air-line distance of over 6000 kilometers (3,700 miles), they must have had their origin much earlier than the Pliocene epoch. This agrees with the conclusions derived from present-day distribution, especially of the American species, that *Crepis* must have originated not later than early Miocene.

Having determined the center of origin and the period in the earth's history when *Crepis* originated, we shall turn in a moment to the story of the origin and development of this group of plants. Before doing so it should be made clear that great care has been taken to ascertain that this hypothetical account of *Crepis* is consistent with the facts and accepted hypotheses of geology, paleontology and floristics. Space forbids an account of this evidence here—it is thoroughly reviewed in the monograph on this genus. The summary statement can be made, that both *Crepis* and its more and more ancient ancestors all could have developed in north central Asia, since the land area from the Altai Mountains to Kamtchatka has been a mountainous continent ever since the Paleozoic era. Also the present continental outlines were established, for the most part, before the middle of the Tertiary period; and the great southern mountain systems from the Himalayas to the Pyrenees, were developing during the Tertiary and Quaternary periods. Lastly, but equally important, Asia was connected with North America and with Europe by continuous land throughout the Miocene, Pliocene and Pleistocene epochs, and with Africa during the Miocene at least. These land bridges were doubtless the migration routes followed in establishing the present world wide distribution of *Crepis.*

Originating presumably in the Altai or eastern Tien-Shan Mountains, the earliest species of *Crepis* probably migrated from the humid areas at lower elevations upward onto the drier steppes, while some of them eventually reached alpine elevations, becoming gradually differentiated in form and structure as they became adapted to more and more diverse environments. During this earliest period of development there must have been a tendency for those species to radiate in all directions. But differences in the environments to which various species had already become adapted would largely determine the directions in which they could migrate most easily. Thus the moisture-loving, lowland species of sections 1 and 5 moved a little northeastward but mostly westward or southwestward; whereas the alpine species of sections 4 and 11 probably jumped along the mountain tops northeastward and eastward as well as southwestward into southern Europe. The alpine *Crepis nana* of section 12 found its way along the mountains into arctic North America; and the same general route, but at lower levels, was taken by the ancestors of section 15. In section 13 one species, the oldest, got as far east as Japan, the next oldest spread from Manchuria to western Europe, and in southern Europe it gave rise to the most advanced member of this section. In section 21, one species got to northeast Asia, two species, along with representatives of sections 8, 17, and 18, moved into southeast Asia, while the fourth species, *C. multicaulis,* spread through south central Asia and westward across Russia to northern Norway where it exists today. All the other species in the genus, or their ancestors, either remained in central Asia (and a few did so) or they took the southwesterly route which brought them eventually into Africa; Asia Minor and the Mediterranean region, where the greatest number of new species have evolved (see Fig. 5).

In bringing this lecture to a close, I should like to discuss briefly the general aspects of evolution in *Crepis.* Three general conditions and three vital processes have been important in the evolution of some 200 species from a few original ones. The first condition is secular. As a rough estimate, the duration of time from early Miocene to the present is probably something like 20 to 30 million years. Although many *Crepis* species are perennial, all of them produce new seed progeny each year. Contemplating 20 to 30 million generations of *Crepis* plants, with a certain chance of successful new types occurring in any generation, one begins to visualize the possibilities for evolution. Furthermore, during this tremendous span of years, the earth has passed through three geological epochs and begun a fourth. Each of these epochs brought gradual but profound changes in environment to which the terrestrial plants had to adapt themselves, or escape by migration, or be wiped out.

The second condition then is environmental change. There are three most important groups of environmental changes. (1) The cooling and drying of the climate in the late Miocene and Pliocene epochs; this induced the general southward trend of migration. (2) The processes of mountain building that recurred from time to time throughout the life of *Crepis* in Southern Eurasia from the Sino-Himalayan region to the Alps, the Pyrenees and the Grand Atlas. These mountain-building processes opened new migration routes for some species and erected barriers for others. The importance of this environmental feature is shown by the fact that sixty per cent. of the endemic species of *Crepis* occur in these mountains, including those of Iran, Asia Minor and the Balkan Peninsula. (3) The effects of glaciation in the Pleistocene epoch, including extreme vacillation in temperature and moisture, especially in the Mediterranean region. It is in the Mediterranean region that we find the greatest concentration of younger species.

The third condition is isolation, which may be accomplished in two ways. Firstly, we note the effect of migration of species which may result eventually in the isolation of populations. Migration may be either altitudinal or horizontal. In either case it makes possible a separation of two or more populations of any one species together with the selective effects of the changed environments into which these populations have moved. Secondly, we recognize the creation of isolation between groups of individuals within any one species by means of genetic changes taking place within the plants themselves. Those mechanical changes in the chromosomes, which led up to reductions in chromosome number from 6 to 5, to 4, to 3, are an effective internal mechanism making for isolation. And, when a change in chromosome number has been finally accomplished, a very effective barrier to the production of fertile offspring has been set up. At an early stage in this speciation process the two new types with different chromosome numbers are not likely to differ at all in external appearance or in normal fertility. This important fact was clearly demonstrated by Miss Gerassimova in her interesting experiment with *Crepis tectorum*. It has also been demonstrated by Dubinin, another Russian, working with the common fruit-fly, *Drosophila melanogaster,* which normally has 4 pairs of chromosomes. Dubinin's new 3-paired form of this fly, which resulted from x-ray experiments, still looks like the normal 4-paired form, but hybrids between the two forms are more or less sterile. Dubinin has proved that the reduction from 4 to 3 pairs of chromosomes in this experiment was accomplished by means of chromosomal interchanges.

Thus we see that the third condition and the first vital process both accomplish the same essential step in the origin of species. The third condition involves the spatial separation of different populations of the same species. The first vital process involves the sexual isolation of different parts of the same population by the creation of an internal mechanism which is capable of becoming more and more complicated and effective as time goes on.

The second vital process is differentiation between isolated populations. In *Crepis* this has been accomplished largely by means of minor gene mutations. It matters little how two parts of the same species become isolated. Whether the separation be spatial or due to an internal mechanism, the recurrence of gene mutations is potentially able to create endless changes in the form and function of the plant and its parts. Some of this differentiation may be non-adaptive. But when natural selection is operating it will tend to be adaptive. Our own research on the genetics of hybrids has shown that gene mutations have certainly brought about the present great diversity of *Crepis* species within the several chromosome number classes, 6, 5, 4 and 3.

The third vital process is adaptation through gene mutation and natural selection. There are several important special adaptations in *Crepis*. One of most profound significance in the evolution of this genus is the change in type of root from the rhizome to the deep taproot. This made it possible for perennial plants to maintain themselves under drier conditions than the oldest species in the genus could endure. From these first deep-rooted perennials many more advanced perennials and all the biennials and annuals have descended. The reduction in length of the life-cycle is another adaptation to xeric conditions which, as we have seen, is correlated with progressive evolution in this genus. This reduction trend has reached its peak in the small, delicate, desert annuals. These plants are specialized for desert conditions not only by their small size, but also by their extreme precocity (they produce flowers and fruits within a few weeks after germination of the seed) and by the longevity of their tiny seeds. Seeds of *Crepis senecioides,* the most advanced type in the whole genus, will germinate after four years or more in storage, whereas seeds of many perennial species will die within one or two years. Special adaptations for distribution of the seeds by the wind are very striking in *Crepis,* particularly the specialized involucre and the development of a long, fine beak on the slender seeds of the most advanced species. Various other special adaptations are found in *Crepis* species.

Now all these specialized types have close relatives which are not so highly specialized and which flourish under less rigorous conditions. The most extreme adaptations in the genus are still connected, through a long series of more and more primitive species, with the oldest members of the genus and their nearest ancestors. Furthermore, our genetic research on many interspecific hybrids has shown that the species crossed differ in numerous genes. In fact the net result of all this research leads to the conclusion that there is no reason to doubt and many reasons to believe that the basic cause of all this evolution through adaptation is gene mutation. The processes of differentiation and adaptation have been slow and gradual. Minor changes in genes have probably caused most of the differences between individuals which have made these adaptations possible. But, with 20 to 30 million generations and millions of plants in each generation, together with changing environments and isolation of populations, there was adequate opportunity for the production of those occasional favorable mutations and of subsequent new combinations of genes which were required for progressive development. All through this long, slow process, the guiding principle which eliminated the unadapted and preserved the adapted individuals must have been none other than natural selection.

We have found that the evolution of *Crepis* rests on three conditions, namely, plenty of time; plenty of environmental changes with the passage of time; and isolation of populations through migration; and on three vital processes: (1) the creation of isolation through changes in chromosome numbers and associated genetic changes; (2) differentiation of species within the several chromosome number groups by means of gene mutations; (3) along with differentiation, adaptation through gene mutation and natural selection.

In answer to the fundamental questions with which we started, we can state with assurance that changes in chromosome number, and the attendant changes in chromosome structure, have been important in creating isolation between groups of individuals within a species; and that these structural changes probably account for the arithmetical series of chromosome numbers found in many genera of animals and plants; but that they have not been important in creating the morphological and physiological differences between species. This differentiation process in the origin of species, we have found, is made possible by the accumulation of gene mutations occurring in already isolated groups or populations.

These two conclusions are in general agreement with most other recent investigations in this field. They are diametrically opposed to the hypothesis of speciation by sudden, profound changes in species. At the same time they contribute to a still broader and firmer foundation for the neo-Darwinian theory of evolution.

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A SUMMARY OF EVIDENCE IN FAVOR OF THE TRACTION FIBER IN MITOSIS

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EVIDENCE has accumulated to the extent that a convincing case can be presented for the theory that chromosomes move during anaphase through the agency of an attached body, the traction fiber. The salient points are included here without any attempt at a historical survey.

EXISTENCE OF FIBERS IN THE LIVING SPINDLE

The occasional reports of spindle fibers seen in living cells do not convince opponents denying their visibility. Striae originating in protoplasmic currents or mitochondrial alignment or the nonhomology of mitotic structure in primitive forms are the alternative explanations offered for the fibrillate appearance (*cf.* Martens, 1930). The living fibers found by Cooper (1941) in the remarkable mitoses of grass-mite blastomeres would probably also be rejected as atypical.

There is a hint of fibrillation in ultraviolet photographs of living spindles (Wyckoff, 1934), but with ordinary light the living spindle appears structureless in nearly all living cells. In such cells, fibers can be made to appear by application of acid (Lewis, 1923), but mitosis is checked until the acid is removed. The constancy of fibrillation in the fixed spindle is good evidence for the almost universal occurrence of a fundamental fibrillar structure of the spindle, but since lines of stress can be made to appear in obviously unorganized materials under a variety of conditions, this evidence requires some reinforcement.

Perhaps the best evidence that spindles are fibrillate previous to contact with fixative comes from experiments with centrifugation (Schrader, 1934) and hypertonicity (Bělař, 1929). Spindles distorted by these agents show upon fixation a fibrillation following the curved axis of the spindle, regardless of the shape it may have assumed. Nor can it be that these agents have of themselves produced a fibrillate coagulation before the distortion, inasmuch as anaphase movement will continue after centrifugation.

Polarized light supplies conclusive evidence that the fundamental structure of the living spindle is fibrillar. Its birefringence is that of a body with longitudinally arranged micellae (Schmidt, 1939; Schmitt, 1939).

This demonstration of the fibrillar structure of the spindle nevertheless does not prove that an individual fiber moves each chromosome. It shows that the necessary entities exist, but they can equally well be called lines of force, lines of flow, or tubes, or even be discounted as bodies without any functional relationship to karyokinesis. Other sources supply us with evidence of fiber participation as against other mechanisms.

AUTONOMY OF CHROMOSOME MOVEMENT

We can immediately eliminate some commonly held hypotheses of the relationship between chromosome and spindle fiber if we consider the behavior of the kinetochore and the independent movement of individual chromosomes. Theories assuming the attraction of the chromosome as a whole, as by an electric charge, or transportation of a passive chromosome in the protoplasm (expanding spindle, currents, shifting viscosity zones, pulsating centrioles) are not consistent with certain phenomena of general occurrence. One is the precession of the kinetochore. Division figures show the kinetochore typically in the lead, and the arms trailing to form the typical V-shape of a centrally attached chromosome. That the kinetochore is actually pulling the chromosome is clearly substantiated by fragmenting the chromosome with x-rays. Acentric fragments move irregularly if at all, and dicentric chromosomes are pulled in two during anaphase. Schaede (1929), favoring the passive carrying of the chromosome, cleverly counters by suggesting that the daughter chromosomes first separate at the kinetochore, thereby allowing that portion to be first pulled toward the poles by the anaphase currents. This, however, is not in keeping with the behavior of irradiation fragments, nor with colchicine mitoses, in which the kinetochores are the last part of the chromosomes to separate once the spindle has been inactivated (Hawkes, 1942).

The other principal obstacle the theories of passive transportation must surmount is the individual movement of chromosomes. The anaphase groups do not migrate as if carried in some general drift of the substrate, but rather move at different rates, start at different times, or even pass each other going in opposite directions. This latter is seen in elongate root cells, or flattened animal cells in tissue culture, following the diagonal orientation of the metaphase plate, and is particularly striking in the crowded mitoses of pollen tubes (Sax and O'Mara, 1941). Autonomy of the chromosomes is undeniably in operation during the elimination of paternal chromosomes in the first spermatocyte of Sciara (Metz, 1936). Here, upon a monocentric mitotic figure, the maternal chromosomes move toward the aster while the paternal chromosomes (with the exception of the limited chromosome) move away from the aster center. Chromosome elimination occurs in others of the fungus flies, and autonomy is not restricted to special organisms. As a general rule, the X chromosome in the heterogametic sex precedes or follows the autosomes. So varied and astonishing are the peculiarities individual chromosomes exhibit in their movements that one can gladly agree with Dr. A. F. Huettner's felicitous characterization, "Chromosomes have sense."

This individuality of chromosome behavior, along with the purposeful functioning of the kinetochore, reveals that between the kinetochore of the chromosome and the pole of the spindle there is a pull which can act selectively on different chromosomes. This eliminates the possibility that the chromosomes are carried in a group by some general change in the cytoplasm, whether this be a current, an expansion of the spindle (phragmoplast), or a progression of zones of gelation. It rules out also the simpler electrostatic theories, in which all chromosomes develop simultaneously a charge over their entire surfaces and move by repulsion and attraction.

REMAINING POSSIBILITIES

This leaves five theory groups which allow for determination of movement by the individual chromosome, in that the initial stimulus can presumably originate in the chromosome. (1) Movement of the chromosome by surface tension differences. (2) An attractive force between kinetochore and spindle pole. (3) Repulsion between daughter kinetochores of each pair. (4) Pushing apart of the daughter kinetochores by an individual "phragmoplast" for each pair. (5) Spindle fiber contraction. We omit ameboid movement, which has sometimes been invoked to explain chromosome movement, although it is an empty term inasmuch as the chromosomes show no pseudopod formation and none of the gel-sol shifts which are involved in true ameboid movement.

Further evidence from centrifugation can eliminate the first three theories. Shimamura (1940) has shown that in a lily pollen mother cell division figure strongly centrifuged (5,000 × g) parallel to the axis of the spindle, the centripetal chromosomes, still held immovably at the kinetochore, form closed V's with the arm considerably stretched. Such a distortion could be interpreted as resulting from marked differences in specific gravity between the central and terminal portions of the chromosome except that centrifugation at right angles to the spindle gives a different alteration of the chromosome. It does not rotate around its own center of gravity, but rather swings around the spindle pole, at some distance from the pole, like a pendulum bob. With ultracentrifuging the results are even more striking. Centrifuging chick embryonic cells at 150,000 × g, Beams and King (1936) were able to tear parts of chromosomes completely away from the spindle, leaving only fragments attached to the spindle halves. These halves had swung as separate entities, so that the chromosomes hung free of any support save the centrifugally directed torn surface of the spindle halves. Gelation of the spindle as a result of extreme centrifugation does not explain the rigid support because parts of the chromosome within the spindle, but not attached to the fiber, were displaced centrifugally.

Shimamura establishes the point that the impression one consistently receives is of a material link between kinetochore and spindle pole, this bond being free to rotate about the pole except for some resistance of the viscous spindle, but not easily stretched. His point is well made, but Schaede (1930) interestingly enough, faced with his own evidence as to the unyielding attachment of the chromosome, concluded *a priori* that a traction fiber would be too fragile to hold the heavy chromosome.

So we are forced to resort to more than a common-sense argument. Consideration of the forces involved gives a more convincing picture. Centrifugation results show that the chromosomes are connected to the pole by a force or structure with a strength greater than that which will distort a chromosome. This is revealed in another manner by dicentric chromosomes (McClintock, 1941, and many x-radiation experiments), which are pulled apart during anaphase. The tensile strength of a chromosome can not as yet be stated in dynes, but its retention of a structural identity through millions of cell generations weighs against any easy frangibility, and one obtains from microdissection the impression that a chromosome is held together by forces considerably beyond the order of magnitude of surface tensions acting on minute bodies. For surface tension to supply the requisite force, we must require the cellular interfacial forces of very limited magnitude to act on one side only of the minute kinetochore, which over its entire surface could not probably develop a force in excess of a thousandth of a dyne. A mathematical comparison of known cellular interfacial tensions with the forces exerted on a centrifuged chromosome would supply the most satisfactory answer to the question of surface tension efficacy. The force on the chromosome can be estimated only when its specific gravity is known, and with further centrifugation experiments and recently developed methods of isolating chromosomes, such data will perhaps become available soon.

Another consideration argues against surface tension and more particularly against an attracting or repelling force acting between kinetochores or between kinetochore and spindle pole. A force strong enough to distort and fragment chromosomes should pull them with more speed than is shown in normal anaphase migration. If we try to explain the slowness as resulting from resistance of the viscous spindle, then we have a situation exactly equivalent to Beams' and King's and Shimamura's centrifugation conditions: opposing forces pulling on different parts of the chromosome. If the spindle retards the arms of the chromosomes with force sufficient to oppose the pull on the kinetochore, stretching of the chromosome should result in normal anaphase, whereas actually we know no such distortion occurs.

In yet another way the concept of an attractive force is incompatible with the dynamics of anaphase movement. Studies of the rate of chromosome movement (Barber, 1939; Ris, 1943) show no increase in velocity as the chromosomes approach the pole, as would be the case were a constant force acting across the space occupied by the spindle. If the force must be assumed to have any properties of an electric or magnetic field, the theory encounters the difficulty of the division figures with crowded or slanting metaphase plates in which chromosomes divide and the daughters move to opposite poles, regardless of the proximity of the pair to one pole. If a force is involved, it must fluctuate, and moreover must be insulated from one pole and directed toward the other!

One can, in place of an attraction, conceive of the motivating force as a repulsion between sister kinteochores, but such a repulsion still does not supply the answer to the discrepancy between magnitude of force and rate of movement. It would in addition require a highly complicated resolution of forces in bent or multipolar mitoses, with the repulsion acting around corners. The possibility is rendered a little more credible by assuming that the spindle is a channeled structure allowing the chromosomes to move only parallel to its axis regardless of the direction of the repelling force. One must ask, however, what could be the nature of a force that could act selectively (autonomously) between each two daughter chromosomes without affecting the others.

Darlington (1936) proposes a channeling of forces along molecular causeways, the spindle fibers, and maintains that as a result of this channeling the chromosome, although repelled only by its sister and the centriole, would be exposed to negligible lateral repulsion. Thus the chromosome can move only toward the waning repulsion of the centriole, pushed by the greater force of the separating kinetochores. Consider, however, that chromosomes converge upon the centriole from the broad metaphase plate. This produces a configuration in which a body motivated by two repulsions acting at an angle less than 180° moves directly against one of the repulsions. This requires a heretofore impossible resolution of forces, and one is hard put to understand how any dielectric properties of water can explain the anomalous mechanics. Note that only the forces are channeled; there is no mechanical guidance of the chromosomes by structures comparable to the spindle tubes of Schrader.

Autonomous repulsion, that is, repulsion only between daughter chromatids, has as its main bugbear the motivation of the unpaired X chromosome in the heterotypic division. Bleier (1931), supporting the chromosome repulsion theory with thought-provoking comparisons between heterosomes and hybrid univalents, proposes an auxiliary agency, the dividing spindle material, which sweeps up the lagging X and carries it to the pole. He overlooks the frequently occurring precession of the heterosome. Moreover, the V shape of a centrally attached X and the loss of acentric fragments require the same participation of the kinetochore as in the autosomes.

Dynamic theories must meet the additional general objection that the karyokinetic figure behaves as a structure, not as a field of force. It can be moved bodily, distorted, split longitudinally or transversely, and even dissected, meanwhile retaining the identity of its parts although the dynamic reltationships are completely deranged. Interruption of mitosis without subsequent disruption, by experimental agents or during the normal process of egg maturation, implies that the chromosomes while moving are in a state of equilibrium. This duality is improbable if only forces separate from structures move the anaphase chromosomes.

It is clear that the strong pull and slow movement during anaphase and the necessity of "beaming" forces in peculiarly selective systems are not compatible with movement emanating from surface tension or with a force acting between two separated bodies. The more complex hypotheses designed to accommodate these difficulties are built on equally untenable contradictions. With the force theories eliminated we are brought to the last group of motive agencies: expanding or contracting structures.

The theory of anaphase movement supplied by an expanding phragmoplast can be harmonized with chromosome autonomy and kinetochore activity if we assume that longitudinal segments of the spindle are activated individually, and push apart the kinetochores of each daughter pair. The theory has some morphological foundation inasmuch as the spindle in some forms can be seen to originate from a grouping of elements that arise singly in connection with each chromosome. Multipolar mitoses and unpaired chromosomes are as damaging to this theory as to its counterpart involving repelling forces. In a multipolar or bent spindle the expanding structure must somehow operate at an angle without buckling. An unpaired meiotic chromosome has no partner to supply a push. Dicentric chromosomes and even separating daughters of a normal chromosome, stretching straight along the spindle axis, leave no space for the hypothetical expanding body, and no points on the chromosome upon which it could obtain purchase. Centrifugation again supplies the final blow. A spindle separated into parallel halves by centrifuging holds both sets of chromosomes against a centrifugal pull, although no trace of a central spindle remains. No adaptation of the repulsion theories, be the agent force or structure, can explain this parallel pull.

The spindle fiber theory encounters no difficulty in those situations which invalidate the other theories. Each fiber, being an independent structure, can contract independently, whether the chromosome be paired or unpaired. A fiber can pull a chromosome to its pole regardless of the number of spindle poles and regardless of the position of the chromosomes in relation to each other. It can exert a pull when curved and when its half spindle is torn entirely away from the other half. Its rate of contraction as evidenced by chromosomal movement is that to be expected of a fiber (Rashevsky, 1941), and the strength of its hold upon the chromosome can be all out of proportion to that rate of movement. Yet the theory retains its original simplicity: a fiber which attaches to a side of the kinetochore and contracts when activated by the chromosome.

Some additional evidence favoring the traction fiber is worth mentioning. When by microdissection one end of a spindle is pulled out of the cell (Wada, 1935), the chromosomes follow, like a bunch of sausages on strings, and fixation after dissection shows the chromosomes connected to the pole by fibers curved in the direction the needle was pulled. Many investigators have shown that physical and chemical agents (especially colchicine) destroy spindle fibers and spindle function simultaneously. Schmidt (1939) has reported that the fibers become less birefringent as anaphase progresses, as if the fiber molecules, rearranging to shorten the fiber, lose some of their longitudinal alignment.

QUESTIONS

What difficulties, then, remain in the way of the traction fiber theory? All the objections can not be removed until the mechanism of chromosome movement is completely understood, but answers to some questions can be set forth tentatively. Some facts considered inconsistent with the theory are not entirely so. A microneedle traversing a spindle does not appear to encounter fibers (Chambers, 1924), but in this case the injury inflicted by the needle may dissolve or weaken the fibers. The fact that chromosomes often override the poles of the spindle is brought against the idea of a structure merely pulling *to* the poles. Elongation of the phragmoplast may account for this, but it is not necessary to rely on this or on cytoplasmic currents for an explanation. Tardy chromosomes being pulled to the poles would be expected to push others ahead of them, even beyond the point of fiber attachment.

Those who object that the spindle fibers have no place to attach seem to consider it necessary for the fiber to attach somewhere outside the spindle, possibly in the cortiplasm. Anaphase movement of chromosomes in spindles displaced by centrifugal force shows that there can be no such external fastening. It is not necessary. The spindle itself is a rigid body braced against stress by its longitudinal structure. Fibers attached at the poles would require no additional anchorage.

The contractility of fibrils needs no defense. Contractility in both animate and inanimate protein fibers has been repeatedly demonstated. Are the same mechanisms involved in contraction of the spindle fiber? As stated above, polarized light shows that molecular rearrangement is involved. A model for such a traction fiber can be seen in the peripheral threads of the unfertilized *Nereis* egg. This fiber, upon contact with the sperm head (chromatin!), contracts and pulls the spermatozoon to the egg surface.

In contesting the other theories of chromosome movement, it is not intended that phenomena upon which some are based are denied. It remains true that the spindle does expand during the division of some kinds of cells and that this expansion exerts considerable pull upon the chromosomes (Upcott, 1938), but we have seen that this can not be the essential mechanism of chromosome movement in most mitoses. Even where the chromosomes are moved by spindle expansion, the fiber apparently acts as an anchor for the chromosomes (Ris, 1943). Similarly, it is undoubtedly true that the chromosome carries an electric charge on its surface, and it seems reasonable that this has something to do with the disposition of the chromosomes, particularly during prophase and metaphase, but this is not the force producing the anaphase movement.

Indispensability of the traction fiber certainly has not been proved as yet. The varieties of mitosis and meiosis are so diverse that one should not be surprised if some were found to lack traction fibers altogether. At present we are safe only in maintaining that the spindle fiber exists and probably is a typical, if not universal, component of the mitotic figure.

NATURE OF THE FIBER

It must be admitted that we are not sure if we have actually seen the fiber which pulls the chromosome. Shaposhnikov (Chapochnikov, 1939) has described short anaphase fibers attached to the chromosome and structurally different from the continuous fibers, and many others have described and drawn fibers connecting chromosome with spindle pole, but the cytological picture among the different organisms and with different methods varies too much for us to say that any one reveals the functioning organelle.

Experimental evidence indicates that from among the micellae or fibrils of the spindle, the chromosome selects or organizes a traction fiber which attaches to opposite sides of the kinetochore. Then, after division of the chromosome, it induces the fiber to contract. Attachment and contraction are separate processes. It was Bělař's idea (1929) that the traction fiber was formed from fluid that spread from the chromosome along the spindle fiber. This permits a chromosomal source of motivation of the fiber, allowing for autonomy. Shivago and Trukhacheva (Schivago and T., 1938) describe just such a liquid kinetic body which spreads along the fiber and then contracts. The traction cone seen in living cells by Fujii and Yasui (reported by Shimamura, 1940) may be of a similar nature.

CONCLUSIONS

There are one or more critical objections to the theories of anaphase movement of the chromosome, with the exception of the traction fiber theory. This theory alone is consistent with the numerous variations of normal mitosis and the evidence of experimental findings without amendments to its original simplicity. It requires merely that the kinetochore of the metaphase chromatid has the power to attach to the fiber approaching on its side of the chromosome and the power to cause that fiber to contract.

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DISTRIBUTION AND VARIATION IN POCKET GOPHERS, *THOMOMYS TALPOIDES*, IN THE STATE OF WASHINGTON II

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CRITERIA FOR THE CLASSIFICATION OF THE GOPHERS OF WASHINGTON

IN estimating the kinship of the various populations of gophers we have relied mostly on characters of color, skull and average size. Characters of skull and size were studied most carefully in the races about Puget Sound. The conclusions drawn from this study seem to apply as well to gophers from other places in Washington.

Color seems less freely responsive to factors of natural selection and microgeographic variation, at least to such as have operated in Washington in post-Wisconsin time, and as a consequence characters of skull and size present differences that better serve to separate populations. Color characters are less variable and often give clues to relationships not otherwise readily apparent. The following comments on color are based on a study of material from the entire state of Washington and not on material from the Puget Sound area alone.

The color pattern of *Thomomys talpoides* is agouti of a simplified type. Both dorsally and ventrally the fur is composed of a single kind of hair, with no differentiation into guard-hair and underfur. The agouti pattern consists of a long, sepia-colored proximal band and a short distal band of yellow to brown. Rarely a third band of pigment is present on the extreme tips of a few hairs in the fur, but it is so short that its effect on the total color is insignificant. This band probably is a vestigial feature and is not treated further in the present report. The amount of color exhibited by the two basic bands of the fur varies with the race.

Until extensive breeding experiments have been carried out with pocket gophers, a completely satisfactory analysis of the genetic factors involved in coat color can not be made. The genetic factors for color, which are discussed in the present report, are those of important systematic value. Storer and Gregory (1934) made a genetic interpretation of certain mutations in color in pocket gophers; they attempted, with considerable success, to relate the abnormal variations to known mutations in color of the rat, mouse, guinea pig and European rabbit.

In considering the problem of color we have found a mutant specimen of *aequalidens* (Mus. Vert. Zool. No. 86955), saved by S. H. Lyman, from Dayton, Columbia County, to be instructive. In it the proximal band is not normal sepia but is colored like, and continuous with, the yellow-brown of the distal band. In this animal the genetic factor for the color of the proximal band seems to be missing. The fact that the color of the distal band was continuous to the base of the fur led us to examine closely other races of pocket gophers. We found that in races in which the color of the distal band was pale, the proximal color was correspondingly pale. If the distal band was dark, the proximal band was dark. Two specimens of *yakimensis,* discussed in detail later, have alternating patches of light-colored and dark-colored fur. The proximal band of the distally light-colored fur is uniformly paler than the proximal band of the distally dark-colored fur. The evidence suggests that the factors for the color of the distal and proximal bands are independent of each other. The distal band seems to be only superficially a band, and to be that portion of the fur in which a pigment, uniformly distributed to the base of the hairs, is not obscured by a darker pigment that is present only proximally. The color of the fur proximally is produced by two pigments, one of which is continuous throughout each hair and one of which is restricted to the proximal part of the fur. When the uniformly distributed pigment is pale (the pallor or darkness can be observed in the distal band), the fur is relatively pale proximally. When the uniformly distributed pigment is dark, the proximal band is darkened by the addition of the more deeply colored uniform pigment. If the proximal pigment be represented by A, and the uniform pigment by B, the actual color of the fur distally would be B, whereas the proximal fur would be A and B. If B is dark, A and B would be relatively darker than when B is pale.

The color of the proximal band of fur of *Thomomys talpoides* may be controlled by genetic factors for a pigment which does not vary in intensity, plus factors for a second pigment which does vary. The sum total of proximal color always varies with this second color which is seen in pure form in the distal band of the fur.

The postauricular patches on *Thomomys talpoides* result from the absence of the segment of the fur that normally bears the distal color. Actual measurement showed the fur of the postauricular patches to be shorter by several millimeters than the surrounding fur. In the mutant specimen of *aequalidens* there are no postauricular patches. The fur of the region usually occupied by the patch is as short as normal but is colored like the distal band. In normal animals the color of the postauricular patch, then, results from the pigment of the proximal band plus the pigment of the distal band. As is to be expected, the postauricular patch is darker in races with dark distal color than in races with pale distal color.

The problem of color in the distal band is more complicated but can probably be explained by assuming a series of multiple alleles. The color varies with each race, from dull yellow in *devexus* to rich chestnut in *aequalidens*. Racial intergrades within subspecific groups assume an intermediate color. In natural crosses between the *fuscus* group of gophers and the *douglasii* group, dominance is revealed. Where *aequalidens* intergrades with *fuscus*, near Pullman, Whitman County, the color is that of *aequalidens* but the cranial characters and external measurements are those of *fuscus*. Intergrades between *aequalidens* and *wallowa* from the Blue Mountains likewise are colored like *aequalidens*, although the size of animal and size and shape of cranium are those of *wallowa*.

The race *yakimensis* seems to possess genes for the color of both *fuscus* and *devexus*, of the *douglasii* group; usually it resembles *fuscus*. Two topotypes of *yakimensis* (W. W. D. Nos. 1076, 1244) show alternate bands of *fuscus*-like color and *devexus*-like color on the back. The gray, *devexus*-like transverse bands are the fewest; they vary from 6 to 30 mm. in anteroposterior length and extend from one side of the animal over the back, to the other side. In every case, these bands *follow molt lines*. Seemingly the dominance of the *fuscus* color can be reversed to that of *devexus* if certain environmental conditions during the molt are suitable. Where *yakimensis* intergrades with *devexus*, the number of *fuscus*-colored individuals becomes progressively less as the range of *devexus* is approached.

The length of the distal color-band along the individual hair is, of course, regulated by relative length of the proximal color. The distal color is continuous to the base but is obscured basally by the proximal color. When the distal band of color of a gopher is short, allowing more of the dark proximal color to show through, the specimen appears darker. The length of the distal band of color is rather constant in each race but varies somewhat from subspecies to subspecies.

Storer and Gregory (*loc. cit.*) reported dutch spotting (partial albinism) in but five pocket gophers. We found no spotting in gophers of the *fuscus* group in Washington, but in every race of the *douglasii* group from the Cascade Mountains westward there is spotting.

In summary, then, study of color in pocket gophers of Washington shows the following important facts: Intergrades of races of the same subspecific group show intermediate color, but crosses between the two groups of subspecies show dominance. There is evidence, in one case at least, that of *yakimensis,* that this dominance is produced by environmental conditions at a critical time. The proximal color of the fur was found to be influenced by the distal color, and therefore is of but little systematic value since its variation in intensity of color parallels that of the distal color. The same is true of the color of the postauricular patches. Color characters of systematic value include: color of the distal band of the fur, relative length of the distal color band, and relative size of the postauricular patches.

In our annotated catalog of races the color is briefly described. The color terms describe the distal band of the fur as it lies on top of the proximal fur, that is, the general color effect of the fur when brushed back. All capitalized color terms are those of Ridgway (Color Standards and Color Nomenclature, 1912). Where a single term applies to the color of two or more subspecies which actually exhibit small but constant differences in color, these differences are mentioned under the heading of *"Comparisons"* in the individual races involved. Where the relative length of the distal band of color plays an important part in the total color effect, that fact is mentioned.

ANNOTATED CATALOG OF RACES

The classification and naming of a group of animals as variable as the pocket gophers of Washington must necessarily be in some measure arbitrary. No rigid definition of a subspecies, based on amount or quality of difference, will suffice. For example, the population of gophers with the "internasal" bone is considered racially akin to the gophers of the same region which lack the bone. Under a rigid system of classification, a character like that provided by the accessory center of ossification might be of ordinal magnitude. In general, however, we have been guided by the following principles:

1. Because no two forms of pocket gophers occupy the same locality in Washington, and since intergradation

occurs where any two kinds come into contact, all pocket gophers in the state are considered as belonging to one species, namely, *Thomomys talpoides*.

2. The pocket gophers of Washington belong to two "subspecific groups" which had different post-Pleistocene histories and genetically are more different from each other than subspecies from within any one group of subspecies are different from each other. It should be emphasized that these groups of subspecies are groups of convenience only, and are not thought of as separate phyletic lines.

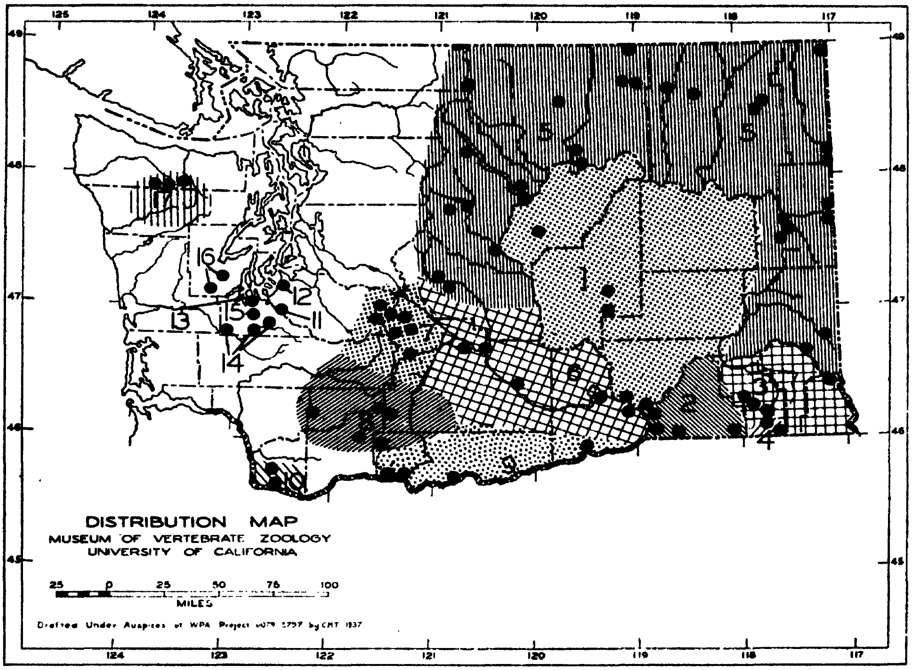

Fig. 5. Distribution of *Thomomys talpoides* in the state of Washington (spots indicate the sources of specimens). 1. *devexus*, 2. *columbianus*, 3. *wallowa*, 4. *aequalidens*, 5. *fuscus*, 6. *yakimensis*, 7. *shawi*, 8. *immunis*, 9. *limosus*, 10. *douglasii*, 11. *glacialis*, 12. *tacomensis*, 13. *pugetensis*, 14. *yelmensis*, 15. *tumuli*, 16. *couchi*, 17. *melanops*.

3. Our conclusions as to the systematic subdivision of the species *Thomomys talpoides* in Washington are summarized in the annotated catalog of races. In designating subspecies, we have considered not only the kind and

degree of difference, but the number of characters that differ. Although cranial characters exhibit greater individual and microgeographic variation than do color characters, the number of cranial characters is so large

TABLE II

AVERAGE MEASUREMENTS OF ADUL MALE *THOMOMYS TALPOIDES* FROM WASHINGTON

Total length	Length of tail	Length of hin	Weight in gra	Condylobasal length	Length of rostrum	Zygomatic breadth	Interorbital breadth	Width of nasals	Width of rostrum
Two *devexus* from 10 mi. S Moses Lake, Grant County									
184	54	25	89	33.7	14.8	20.3	6.6	4.2	7.3
One *devexus* from 4 mi. W Pasco, Franklin County									
224	70	27	105	36.3	17.5	22.6	6.5	4.8	7.8
Five *columbianus* from Touchet, Walla Walla County									
213	60	29	...	37.2	17.2	22.2	7.1	4.5	7.7
Three *columbianus* from 1 mi. E Junction of Snake and Columbia Rivers, Walla Walla County									
211	72	27	122	37.4	17.5	22.6	6.7	4.3	8.2
Four *aequalidens* from 5–6 mi. SE Dayton, Columbia County									
202	57	26	...	37.4	16.7	23.2	6.9	4.6	7.8
Four *wallowa* from Mountain Top and Stay-a-while Springs, Columbia County									
191	56	26	82	33.6	15.3	20.4	6.7	4.0	6.8
Three *fuscus* from Newport, Pend Oreille County									
189	54	27	...	34.4	16.2	20.3	6.3	4.4	6.7
Four *fuscus* from Conconully, Okanogan County									
191	50	26	...	34.2	16.0	19.6	6.3	4.3	6.8
Four *yakimensis* from Selah, Yakima County									
209	60	27	...	34.3	15.8	21.3	6.2	4.2	6.9
Two *shawi* from Mount Rainier, Pierce County									
227	72	32	...	38.1	17.3	22.2	6.9	4.5	7.3
Two *immunis* from Morrison Springs Ranger Station, Skamania County									
211	64	28	102	36.2	17.2	22.0	6.8	4.6	7.8
One *limosus* from White Salmon, Klickitat County									
210	55	30	...	36.2	16.6	21.2	6.5	4.5	7.4
Two *douglasii* from 5 mi. E Vancouver, Clark County									
227	68	30	148	38.3	18.1	23.7	7.7	5.4	8.5
Twenty *glacialis* from 2 mi. S Roy, Pierce County									
225	72	31	128	37.9	17.7	23.0	6.6	4.3	8.1
Thirteen *tacomensis* from 5 mi. SW Tacoma, Pierce County									
224	71	31	127	37.5	17.0	21.9	6.5	4.5	8.1
Fourteen *pugetensis* from 4 mi. S Olympia, Thurston County									
223	62	30	123	37.0	17.9	22.4	6.6	4.2	7.8
Eleven *tumuli* from 7 mi. N Tenino, Thurston County									
225	30	31	140	37.7	17.1	22.0	6.4	4.5	7.9
Twelve *yelmensis* from 1 mi. W Vail, Thurston County									
216	62	30	126	36.2	17.6	21.3	6.8	4.2	8.0
Twenty-one *yelmensis* from 1 mi. S Tenino, Thurston County									
213	64	29	121	36.8	17.6	21.7	6.5	4.3	7.7
Sixteen *yelmensis* from 2 mi. N Rochester, Thurston County									
215	63	30	117	36.3	17.6	21.1	6.9	4.1	7.3
Thirteen *couchi* from 4 mi. N Shelton, Mason County									
196	55	27	87	34.5	16.4	20.3	6.2	4.0	7.3
One *melanops* from Happy Lake Ridge, Callam County									
211	67	28	...	36.6	16.9	21.5	6.2	4.0	7.8

TABLE III

AVERAGE MEASUREMENTS OF ADULT FEMALE *THOMOMYS TALPOIDES* FROM WASHINGTON

Total length	Length of tail	Length of hind foot	Weight in grams	Condylobasal length	Length of rostrum	Zygomatic breadth	Interorbital breadth	Width of nasals	Width of rostrum
Four *devexus* from 10 mi. S Moses Lake, Grant County									
184	55	25	71	31.6	14.3	18.7	6.4	4.7	6.6
Six *devexus* from 4 mi. W Pasco, Franklin County									
198	64	26	89	33.5	15.6	19.9	6.6	4.5	7.0
Three *columbianus* from Touchet, 450 ft., Walla Walla County									
109	58	28	...	35.8	16.0	21.8	6.9	4.6	7.4
Three *columbianus* from Wallula, Walla Walla County (approaching *devexus*)									
197	62	27	97	33.4	14.7	19.5	6.6	4.1	7.0
Four *columbianus* from 1 mi. E Junction Snake and Columbia Rivers, Walla Walla County									
203	61	28	96	34.8	16.1	21.2	6.7	4.2	7.0
One *aequalidens* from 5 mi. S Dayton, Columbia County									
201	59	27	...	36.7	16.2	22.0	7.0	4.6	7.8
Four *wallowa* from Mountain Top and Hompeg Falls, Columbia County									
180	52	25	...	31.8	14.6	20.1	6.5	4.2	6.7
Two *fuscus* from Newport and 8 mi. S Newport, Pend Oreille County									
186	57	26	76	34.5	16.6	19.8	6.8	4.0	6.9
Six female *fuscus* from Conconully, Okanogan County									
186	53	26	...	33.1	15.1	18.6	6.2	4.0	6.5
Three *yakimensis* from Selah, Yakima County									
191	56	25	...	32.1	15.7	19.7	6.2	4.2	6.7
Seven *shawi* from vicinity of Mount Rainier, Pierce County									
213	64	30	...	36.1	16.9	21.3	6.7	4.2	7.6
Eight *immunis* from 5 mi. S Troutlake, Klickitat County									
214	61	28	105	36.0	17.3	21.3	7.0	4.3	7.7
Two *immunis* from Morrison Springs Ranger Station, Skamania County									
212	58	29	101	35.6	17.2	20.9	6.6	4.4	7.6
Thirteen *limosus* from White Salmon, Klickitat County									
198	56	28	86	34.6	15.9	21.1	7.0	4.3	7.4
Ten *douglasii* from 5 mi. E Vancouver, Clark County									
213	63	30	117	36.5	17.2	21.7	7.3	4.5	8.0
Seventeen *glacialis* from 2 mi. S Roy, Pierce County									
220	71	30	116	37.1	17.5	22.2	6.4	4.0	8.0
Fifteen *tacomensis* from 5 mi. SW Tacoma, Pierce County									
196	57	29	104	35.7	16.4	20.8	6.5	4.1	7.7
Nineteen *pugetensis* from 4 mi. S Olympia, Thurston County									
205	59	29	96	35.6	16.2	21.1	6.4	4.0	7.4
Fourteen *tumuli* from 7 mi. N Tenino, Thurston County									
216	64	30	118	36.7	16.5	21.4	6.5	4.6	7.6
Ten *yelmensis* from 1 mi. W Vail, Thurston County									
211	63	30	107	35.7	16.6	20.8	6.6	4.4	7.8
Twenty-one *yelmensis* from 1 mi. S Tenino, Thurston County									
202	61	28	101	35.7	16.6	20.4	6.2	4.1	7.4
Thirteen *yelmensis* from 2 mi. N Rochester, Thurston County									
203	62	29	101	35.3	16.3	20.7	6.8	4.1	7.5
Nine *couchi* from 4 mi. N Shelton, Mason County									
191	53	27	79	33.8	15.6	19.7	6.0	3.9	7.1
Five *couchi* from Lost Lake Prairie, Thurston County									
189	56	26	81	33.7	15.5	19.5	6.0	3.8	7.4

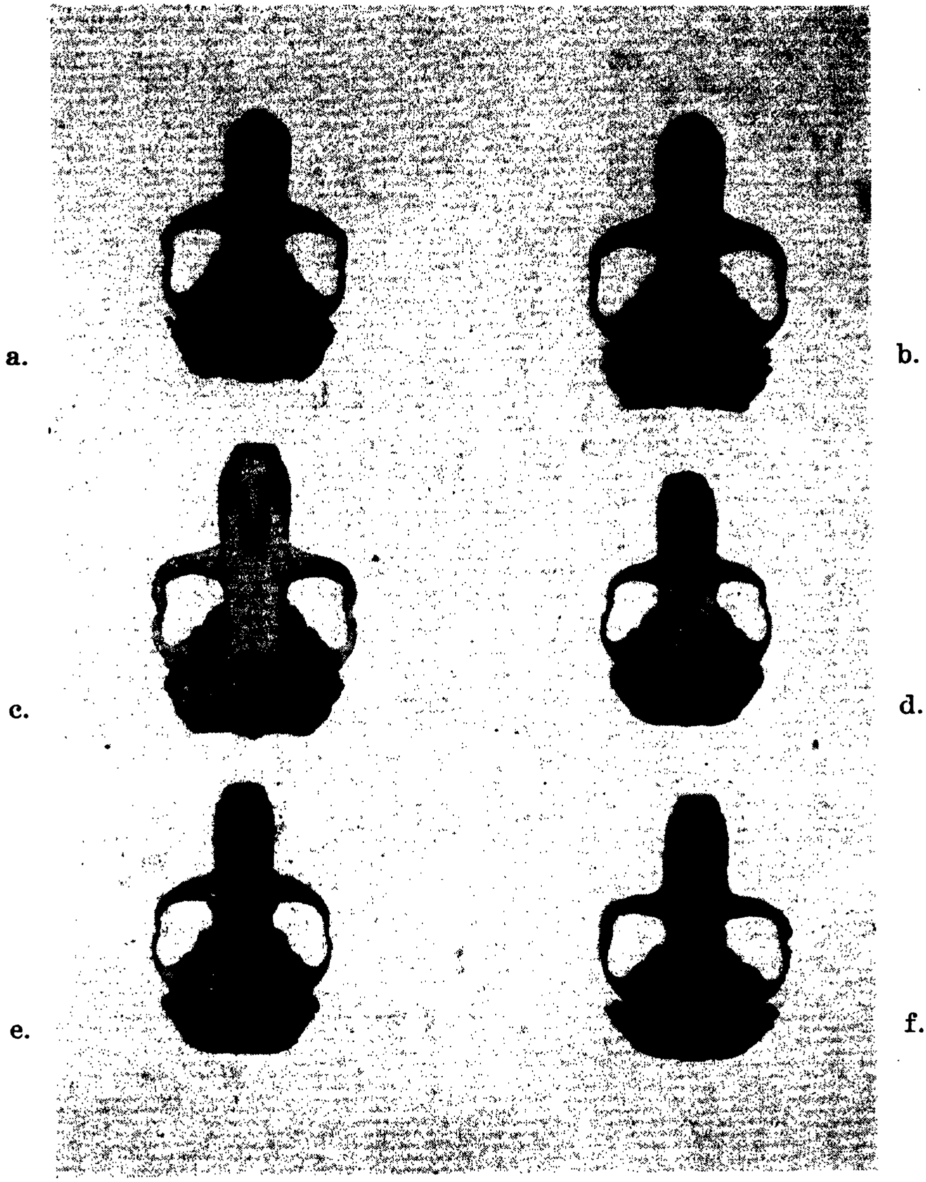

Fig. 6. Skulls of adult male *Thomomys talpoides* from Washington (natural size). a. *devexus*, 10 mi. S Moses L., Grant Co. (No. 835 VBS); b. *columbianus*, topotype (No. 44911 MVZ); c. *aequalidens*, topotype (No. 66403 MVZ); d. *wallowa*, Stay-a-while Springs, Columbia Co. (No. 87196 MVZ); e. *fuscus*, Pass Creek Pass, Pend Oreille Co. (No. 959 WWD); f. *yakimensis*, topotype (No. 1246 WWD).

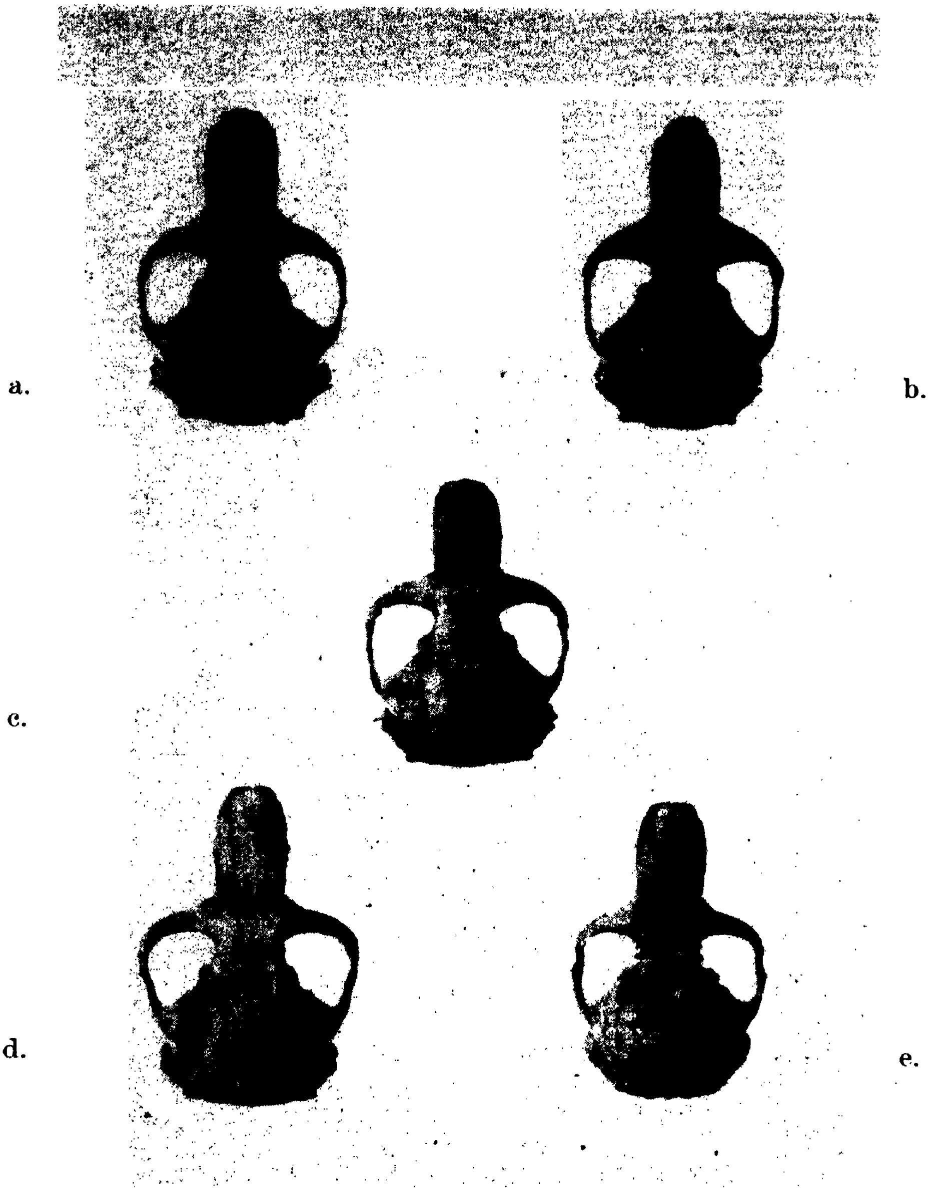

FIG. 7. Skulls of adult male *Thomomys talpoides* from Washington (natural size). a. *shawi*, Dewey Lake, Yakima Co., (No. 1923 WWD); b. *immunis*, topotype, (No. 2267 WWD); c. *limosus*, topotype, (No. 2249 WWD); d. *douglasii*, topotype, (No. 2241 WWD); e. *melanops*, topotype, (No. 241942 BSC).

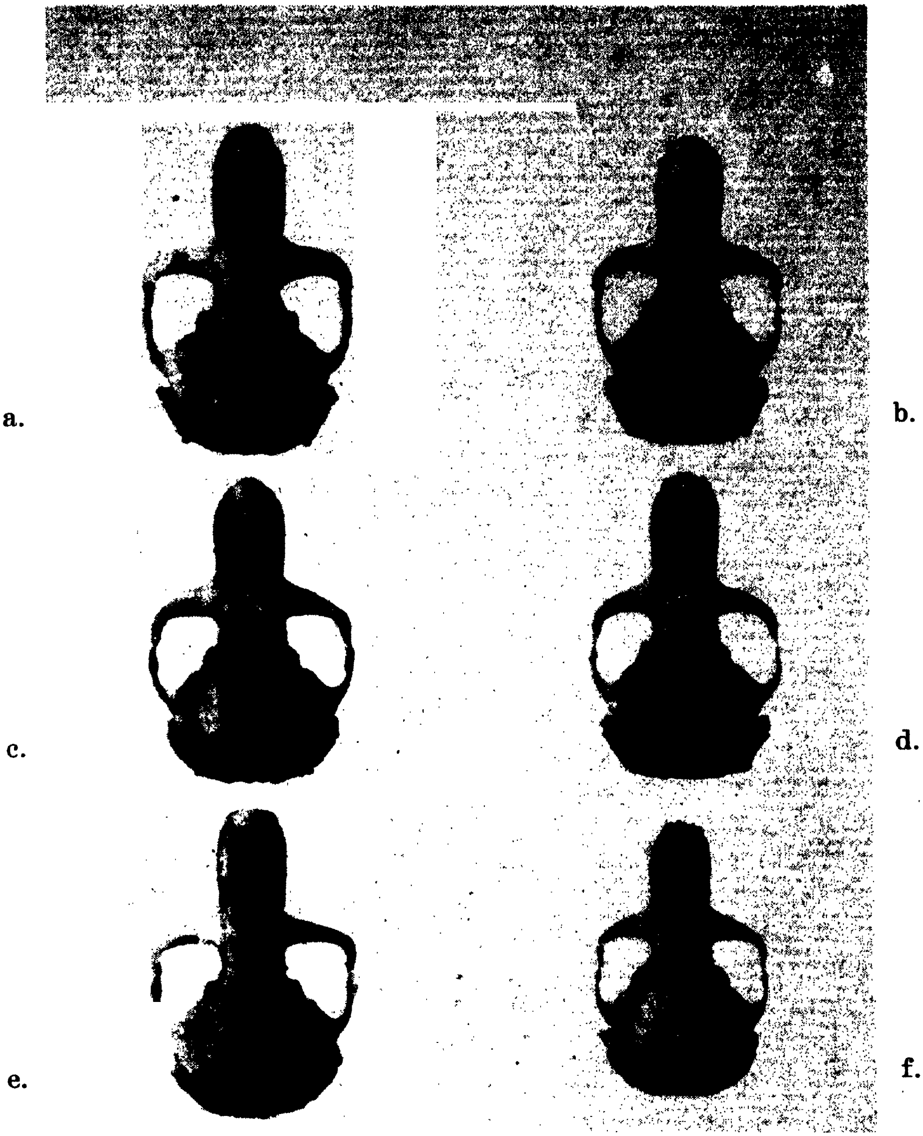

FIG. 8. Skulls of adult male *Thomomys talpoides* from Washington (natural size). a. *glacialis*, topotype, (No. 2756 WWD); b. *tacomensis*, 5 mi. SW Tacoma, Pierce Co., (No. 1973 WWD); c. *pugetensis*, topotype, (No. 2019 WWD); d. *tumuli*, topotype, (No. 2777 WWD); e. *yelmensis*, topotype, (No. 2131 WWD); f. *couchi*, Lost Lake Prairie, Mason Co., (No. 1993 BSC).

that measurements of the skull furnish the best criteria for the separation of gophers. Cranial features of all races occurring in Washington are shown in Figures 6, 7 and 8. Cranial measurements of systematic value are given in Tables II and III. Of all characters, those of body size seem to be most subject to individual and microgeographic variation, and most responsive to rapid selection and most prone to rapid evolution. Size, expressed by external measurements and weights, is recorded in Tables II and III.

The order of arrangement of the following systematic accounts of subspecies is one that permits comparison most readily of any one subspecies with geographically adjacent races. The list begins with *Thomomys t. devexus* from the Columbian Plateau of central eastern Washington, and is followed by *columbianus,* the race with which it intergrades on the south. After *columbianus,* races are listed in order, east to the Idaho boundary, then north to the Canadian boundary, then west to the Cascade Mountains, and then south along the Cascades to Mount Rainier, the range of *shawi.* Following *shawi,* races to the south are discussed until *douglasii* is reached. After *douglasii,* races to the west of *shawi,* in the Puget Sound area and the Olympic Mountains, are discussed. The arrangement of specimens examined follows the above order, first by county and second by localities within each county.

Comparisons of color are given under each subspecies heading and comparisons are restricted to races with adjoining geographic ranges or similar color. Comparisons of skulls and measurements are presented most briefly in tabular and graphic form (Tables II and III, Figs. 6, 7 and 8).

Thomomys talpoides devexus Hall and Dalquest

Thomomys talpoides devexus Hall and Dalquest, *Murrelet,* Vol. 20, p. 3, April 30, 1939.

Thomomys talpoides ericaeus Goldman, *Jour. Mamm.,* Vol. 20, p. 243, May 14, 1939. Type from Badger Mountains, Douglas County, Washington.

Type. Adult male, skin and skull, No. 84517, Mus. Vert. Zool., obtained 1 mi. WSW Neppel (now Moses Lake), Grant County, Washington, by W. W. Dalquest, May 30, 1938; original No. 688.

Range. The Columbian plateau of central eastern Washington.

Intergradation. Intergradation between *devexus* and *yakimensis* takes place at the mouth of the Yakima River, near Richland, Benton County. Intergradation with *fuscus* probably occurs along the eastern border of the range of *devexus.* Specimens from along the Columbia River in Walla Walla County show approach to *devexus* in pale grayish color. Indeed, specimens from southern Franklin County, on the southeastern corner of the Columbian plateau, show some approach to *columbianus* in large size and heavy skulls, representing an extreme microgeographic race or indicating that some individuals of *columbianus* have crossed the Snake River and entered the range of *devexus.* The pale color of certain specimens from the Columbia River Valley in eastern Benton County indicates some infusion of *devexus* blood into the population on this side of the river.

Color. Adult topotypes in fresh summer pelage are near Cinnamon-Buff in color.

Comparisons. This small race is the palest of Washington gophers. It is distinctly paler and grayer than *columbianus* or any other race with adjoining geographic range.

Remarks. The gray color of *devexus* best serves to distinguish it from other races of gophers. Specimens from both north and south of the type locality are larger over all and have larger skulls than topotypes.

Specimens examined. Total number 26, as follows: *Douglas Co.*: Badger Mountains, 2 (WSM).* *Grant Co.*: 1 mi. WSW Moses Lake, 1 (type); The Potholes, 10 mi. S Moses Lake, 7 (WWD 4, BSC 3). *Franklin Co.*: 4 mi. W Pasco, 350 ft., 15 (MVZ); 2½ mi. E, 1½ mi. S Pasco, 400 ft., 1 (MVZ).

* Names of collections are designated as follows:

BSC—Biological Surveys Collection, National Museum, Washington, D. C.
CRC—Charles R. Conner Museum, Pullman, Wash.
MVZ—California Museum of Vertebrate Zoology, Berkeley.
WSM—Washington State Museum, Seattle.
WWD—Walter W. Dalquest Collection, Berkeley.

Thomomys talpoides columbianus Bailey

Thomomys fuscus columbianus Bailey, *Proc. Biol. Soc. Wash.*, Vol. 27, p. 117, July 10, 1914.

Thomomys columbianus Bailey, *N. Amer. Fauna* 39, p. 106, November 15, 1915.

Thomomys talpoides columbianus Goldman, *Jour. Mamm.*, Vol. 20, p. 234, May 14, 1939.

Type. Adult male, No. 23722, U. S. Nat. Mus., Biol. Surv. Coll., obtained by C. P. Streator at Touchet, Walla Walla County, Washington, September 10, 1890; original No. 234.

Range. Walla Walla County, Washington, from the Columbia River east to the boundary of Columbia County, and from the Snake River south to the Oregon boundary.

Intergradation. Intergradation with *devexus* occurs along the Columbia River in western Walla Walla County. Intergradation with *wallowa* probably takes place in extreme southeastern Walla Walla County. Intergradation with *aequalidens* occurs at Dixie, Walla Walla County.

Color. Adult topotypes in fresh summer pelage are near Ochraceous-Orange in color.

Comparisons. This is the brightest and warmest-colored of Washington gophers. It can scarcely be confused with the dark *aequalidens* to the east. It is somewhat like *yakimensis* in color, but is paler and less glossy, with shorter distal color bands on the fur. The skull is larger and heavier than that of *yakimensis* or *fuscus*, with more angular, flaring zygomatic arches. Comparison with *devexus* is made under the account of that race.

Remarks. Along the Columbia River *columbianus* is especially gray in color, thus showing an approach to *devexus*. To the east, as the range of *aequalidens* is approached, *columbianus* becomes considerably darker.

Specimens examined. Total number 34, as follows: *Walla Walla Co.*: Touchet, 450 ft., 11 (MVZ); 7 mi. S Dixie, 4300 ft., 5 (MVZ); Prescott, 2 (approaching *aequalidens*) (MVZ); 2 mi. E junction Snake and Columbia rivers, 350 ft., 1 (approaching *devexus*) (MVZ); 1 mi. E junction Snake and Columbia rivers, 12 (approaching *devexus*) (MVZ); Wallula, 3 (approaching *devexus*) (MVZ 1, BSC 1, WWD 1).

Thomomys talpoides aequalidens Dalquest

Thomomys talpoides aequalidens Dalquest, *Murrelet*, Vol. 23, p. 3, May 14, 1942.

Type. Adult male, No. 66403, Mus. Vert. Zool., obtained at Abel Place, 220 ft., 6 mi. SSE Dayton, Columbia County, Washington, by S. H. Lyman, April 6, 1934; original No. M–28.

Range. Southeastern Washington east of the range of *columbianus*, exclusive of the Blue Mountains (see Fig. 5).

Intergradation. Intergradation with *fuscus* is shown by specimens here referred to that race from Pullman and Wawawai. Intergradation with *wallowa* occurs throughout the Blue Mountains of Washington. Intergradation with *columbianus* takes place near Dixie.

Color. Adult topotypes in fresh summer pelage are near Cinnamon-Brown in color.

Comparisons. This is the darkest race in eastern Washington. Specimens intermediate between *aequalidens* and the *fuscus*-group of gophers (*wallowa* and *fuscus*), resemble *aequlidens* in color but may be separated by their smaller size and smaller, less angular skulls and less flaring zygomatic arches. The occipital condyles of *wallowa* extend much farther posteriorly to the mastoid region than they do in *aequalidens.*

Remarks. The existence of this dark-colored gopher in an area possessing generally pale-colored mammalian races indicates the weakness of natural selective factors for color; at least such as have operated in post-Wisconsin time.

Specimens examined. Total number 16, as follows: *Columbia Co.*: Dayton, 1600 ft., 4 (MVZ); 5 mi. SE Dayton, 2150 ft., 3 (MVZ); 6 mi. SSE Dayton, 2200 ft., 4 (MZV); Jim Creek, 3200 ft., 11 mi. SE Dayton, 4 (MVZ). *Asotin Co.*: Clarkston, 1 (CRC).

Thomomys talpoides wallowa Hall and Orr

Thomomys quadratus wallowa Hall and Orr, *Proc. Biol. Soc. Wash.*, Vol. 46, p. 41, March 24, 1933.

Thomomys talpoides wallowa Goldman, *Jour. Mamm.*, Vol. 20, p. 234, May 14, 1939.

Type. Adult male, skin and skull, No. 54701, Mus. Vert. Zool., obtained at Catherine Creek, 7 mi. E. Telocaset, 3500 ft., Union County, Oregon, by R. T. Orr, June 29, 1932; original No. 570.

Range. Blue Mountains of southeastern Washington.

Intergradation. All the specimens examined from Washington are, to a greater or lesser degree, intergrades between *wallowa* and *aequalidens,* although the specimens from the range assigned to *wallowa* in Washington (see Fig. 5) are referable to *wallowa.*

Color. Adult topotypes in fresh summer pelage are near Ochraceous-Tawny in color. Most of the specimens from Washington are colored like *aequalidens.*

Comparisons. At the type locality, *wallowa* is colored like *fuscus.* Other than in color, the chief differences separating Washington specimens of *wallowa* from *fuscus* are: smaller size, smaller and weaker skull and occipital condyles ending relatively farther posteriorly to the mastoid region.

Specimens examined. Total number 10, as follows: *Columbia Co.*: Mountain Top, 4500 ft., 5 (MVZ); Twin Buttes Ranger Station, 25 mi. SE Dayton, 1 (MVZ); Stay-a-while Spring, 3 (MVZ); Hompeg Falls, 1 (MVZ).

Thomomys talpoides fuscus Merriam

Thomomys clusius fuscus Merriam, *N. Amer. Fauna* 5, p. 69, 1891.

Thomomys myops Merriam, *Proc. Biol. Soc. Wash.,* Vol. 14, p. 112, July 19, 1901. Type from Conconully, Okanogan County, Washington.

Thomomys fuscus fuscus Bailey, *N. Amer. Fauna* 39, p. 126, November 15, 1915.

Thomomys talpoides fuscus Hall and Dalquest, *Murrelet,* Vol. 20, April 30, 1939.

Type. Adult female, No. 24267, U. S. Nat. Mus., Biol. Surv. Coll., obtained from the mountains at the head of Big Lost River, Custer County, Idaho, by B. H. Dutcher, September 23, 1890; original No. 1847.

Range. The eastern part of the state, from Pullman, Whitman County, north to the Canadian boundary, and in the northern part of the state west, north of the Columbia River, to the Cascade Mountains, and thence south, west of the Columbia River, to Wenatchee and Merritt, Chelan County.

Intergradation. Intergradation of *fuscus* with *devexus* probably takes place along the eastern edge of the range of the latter race, but is not shown in specimens at hand. Intergradation with *yakimensis* takes place in the Wenatchee Mountain area (Lake Cle Elum, Kittitas County; Merritt and Wenatchee, Chelan County). Intergradation with *aequalidens* is shown in specimens from Pullman and Wawawai, Whitman County.

Color. Adult topotypes in summer pelage are near Ochraceous-Tawny. Washington specimens average slightly duller than the series of topotypes available to us.

Comparisons. This race is smaller and slightly browner, less orange in color, than *yakimensis.* Comparisons with *fuscus* and *wallowa* are made in accounts of those races.

Remarks. The range tolerance of this race is wide; edaphic or ecologic features that might serve as barriers to other races do not restrict *fuscus.* This is thought to account, in part, for the wide geographic range of *fuscus* in Washington, and for the few microgeographic races.

The name *myops* Merriam, proves to be based on a microgeographic race which does not differ in color, and differs but slightly in cranial characters, from typical *fuscus.* In all topotypes of *myops* at hand, the premaxillae extend little or not at all past the posterior end of the nasals. This character is variable over the range of *fuscus* in Idaho and Washington.

Specimens examined. Total number 92, as follows: *Whitman Co.*: Wawawai, 1 (CRC); Pullman, 8 (CRC). *Spokane Co.*: Cheney, 1 (BSC); Liberty Lake, 2 (BSC); Marshall, 9 (BSC); Spokane Falls, 6 (BSC); Spokane Bridge, 3 (BSC). *Pend Oreille Co.*: 8 mi. S Newport, 1 (WWD); 2 mi. S Newport, 1 (WWD); Newport, 5 (WWD 3, MVZ 1, BSC 1); Round Top Mountain, 2 (CRC 1, WWD 1). *Ferry Co.*: Sherman Creek Pass, 1 (WWD); 2 mi. E Republic, 1 (WWD). *Stevens Co.*: 5 mi. W Pend Oreille Lake, 1 (WWD); 15 mi. E Colville, 3 (BSC). *Okanogan Co.*: 20 mi. E Tonasket, 3 (WWD); 15 mi. E Tonasket, 5 (WWD); Chesaw, 1 (WSM); 6 mi. SE Okanogan, 1 (WWD); Duley Lake, 1 (WWD); Conconully, 3280 ft., 11 (MVZ). *Chelan Co.*: S end Lake Chelan, 2 (WWD); 3 mi. W Chelan, 1 (WSM); Lakeside, 1 (WSM); Lucerne, 1 (CRC); Lake Wenatchee, 1 (CRC); Wenatchee, 3 (WWD 2, CRC 1); Merritt, 12 (WWD 10, MVZ 2).

Whatcom Co.: Barron, 1 (CRC). *Kittitas Co.*: 5 mi. NW Cle Elum, 3 (WWD).

Thomomys talpoides yakimensis Hall and Dalquest

Thomomys talpoides yakimensis Hall and Dalquest, *Murrelet*, Vol. 20, p. 4, April 30, 1939.

Thomomys talpoides badius Goldman, *Jour. Mamm.*, Vol. 20, p. 242, May 14, 1939. Type from Wenatchee, Chelan County, Washington.

Type. Adult female, skin and skull No. 84518, Mus. Vert. Zool., obtained at Selah, Yakima County, Washington, by Peggy Burgner, November 27, 1938; original No. 1077 of W. W. Dalquest.

Range. The Yakima Valley area, east to the Columbia River, north to the Wenatchee Mountains, west to the Cascade Mountains, and south probably to the Simcoe Range.

Intergradation. Intergradation between *yakimensis* and *devexus* takes place at the mouth of the Yakima River. Intergradation with *fuscus* occurs over a rather wide area, from Cle Elum, Kittitas County, north to Merritt and Wenatchee, as might be expected from the migrational history of the two races. Intergradation with *shawi* occurs in the western foothills of the Cascade Mountains. Intergradation with *limosus* may take place on the northern slope of the Simcoe Range; gophers are not certainly known to occur there.

Color. Adult topotypes in fresh summer pelage are near Ochraceous-Tawny in color, and are slightly brighter and more orange than *fuscus*.

Comparisons. Compared with *shawi*, *yakimensis* is smaller and is orange, rather than dark grayish-brown in color. Comparisons with *fuscus* are made in the account of that race.

Remarks. The racial stock of *yakimensis* appears to have been a mixture of gophers of the *douglasii* group (*T. t. devexus*) and the *fuscus* group (*T. t. fuscus*) which, isolated in the Yakima Valley, subsequently deviated from both ancestral types.

Specimens examined. Total number 43, as follows: *Yakima Co.*: Selah, 18 (WWD 11, WSM 5, MVZ 2); Cowiche, 3 (MVZ); Zillah, 1 (CRC). *Benton Co.*: 2 mi. NW Richland, 400 ft., 1 (MVZ); S side of Yakima River, 2 mi. SE Richland, 9 (MVZ); 3 mi. W, 1 mi. N Kennewick, 375 ft., 11 (MVZ).

Thomomys talpoides shawi Taylor

Thomomys douglasii shawi Taylor, *Proc. Biol. Soc. Wash.*, Vol. 34, p. 121, June 30, 1921.

Thomomys talpoides shawi Hall and Dalquest, *Murrelet*, Vol. 20, p. 4, April 30, 1939.

Type. Adult male, skin and skull, No. 232807, U. S. Nat. Mus. Biol. Surv. Coll., obtained at Owyhigh Lakes, Mount Rainier, Pierce County, Washington, by G. G. Cantwell, August 9, 1919; original No. 1464.

Range. The central Cascade Mountains, from Mount Rainier south certainly to Signal Peak.

Intergradation. Intergradation between *shawi* and *immunis* probably occurs somewhere north of Mount Adams, but is not shown in material at hand. Intergradation with *yakimensis* takes place in the eastern foothills of the Cascades in Yakima County. No intergradation with *glacialis* occurs at the present time.

Color. Adult topotypes in fresh summer pelage are near Tawny in color.

Comparisons. This race is slightly paler and less rich in color than *immunis*. Comparisons with *yakimensis* are made in the account of that form.

Remarks. The separation of *shawi* and *immunis* seems to have been brought about by ecologic barriers. The habitat occupied by *shawi* consists of damp alpine meadows at considerable elevation, while *immunus* is found usually in dry, grassy clearings in open pine woods. Unfortunately, the major parts of the supposed ranges of both lie in rugged, inaccessible country. The habitat preferences of *shawi* were studied only on Mount Rainier, the northern border of its range; those of *immunis* were studied only in the southern part of its range, near Mount Adams.

Specimens examined. Total number 27, as follows: *Yakima Co.*: Goose River at Bumping River, 1 (CRC); 3 mi. NE Goose Prairie, Bumping Lake, 1 (BSC); McAllister Meadows, 2000 ft., 2 (BSC); McAllister Meadows, 2900 ft., 1 (CRC); S fork, Tieton River, 1 (CRC); head of Hindoo Creek, Mt. Aix, 6500 ft., 1 (BSC); Twin Sisters Lakes, 5300 ft., 1 (BSC); 2 mi.

SW Conrad Meadows, 4200 ft., 2 (BSC); Signal Peak, 4000 ft., 5 (BSC); Yakima Indian Reservation, 1 (BSC). *Pierce Co.*: Glacier Basin, 5935 ft., Mount Rainier, 5 (BSC, 4, CRC, 1); Owyhigh Lakes, 5100 ft., Mount Rainier, 3 (BSC, 2, CRC, 1); Dewey Lake, 3 (WWD).

Thomomys talpoides immunis Hall and Dalquest

Thomomys talpoides immunis Hall and Dalquest, *Murrelet*, Vol. 20, April 30, 1939.

Type. Subadult male, skin and skull, No. 84519, Mus. Vert. Zool., obtained 5 mi. S Trout Lake, Klickitat County, Washington, by W. W. Dalquest, July 27, 1937; original No. 395.

Range. From Trout Lake north, at least to Mount Adams.

Intergradation. Intergradation between *immunis* and *limosus* probably occurs less than 10 miles north of the Columbia River in higher land away from the river-valley meadows, a place from which no specimens are available. None of the specimens examined show intergradation.

Color. Adult topotypes in fresh summer pelage are near Tawny in color.

Comparisons. This race is paler and grayer than either *shawi* or *limosus.* The skull of *immunis* is larger and relatively longer than that of *limosus,* with flaring zygomatic arches (see Fig. 7).

Remarks. The northern, western and eastern boundaries of the range of this race can not be ascertained at present because of the lack of specimens from some critical but inaccessible places. Probably the range extends west of Mount St. Helens and east to the Simcoe Range.

Specimens examined. Total number 27, as follows: *Yakima Co.*: Gotchen Creek Ranger Station, 1 (CRC). *Klickitat Co.*: 5 mi. S Trout Lake, 9 (WWD). *Skamania Co.*: 1 mi. S Morrison Springs Ranger Station, 7 (WWD); Twin Buttes, 4300 ft., 2½ mi. SW Steamboat Mountain, 2 (MVZ); Cayuse Meadows, 3½ mi. SW Steamboat Mountain, 3800 ft., 5 (MVZ); Mount St. Helens, 3 (BSC).

Thomomys talpoides limosus Merriam

Thomomys limosus Merriam, *Proc. Biol. Soc. Wash.*, Vol. 14, p. 116, July, 1901.

Thomomys talpoides limosus Goldman, *Jour. Mamm.*, Vol. 20, p. 235, May 14, 1939.

Type. Adult male, No. 89724 U. S. Nat. Mus., Biol. Surv. Coll., obtained at White Salmon, Klickitat County, Washington, by J. A. Loring, June 26, 1897; original No. 4382.

Range. The Columbia River Valley from Paterson, Benton County, east to White Salmon, Klickitat County. Probably found also on the southeastern part of the Simcoe Range.

Intergradation. Intergradation between *devexus* and *limosus* occurs as far west as Paterson, Benton County. Intergradation with *immunis* must take place less than 10 miles north of White Salmon, Klickitat County. No intergradation with *douglasii* is apparent.

Color. Adult topotypes in full summer pelage are near Tawny in color.

Comparisons. Compared with *shawi*, *limosus* is slightly paler. Compared with *immunis*, *limosus* is considerably darker. Compared with *douglasii*, *limosus* is less yellow.

Remarks. *T. t. limosus* seems to be the western counterpart of *aequalidens*, which it closely resembles. Increased aridity is thought to have caused the removal of the Simcoe Bridge (see account of immigrational history) in the Columbia River Valley, thus isolating *aequalidens* in southeastern Washington and *limosus* on the Simcoe Range, west of the Columbia River. This same aridity is thought to have created conditions in the lower Columbia Valley favorable to the spread of gophers, and to have allowed *limosus* to spread westward as far as the type locality.

Specimens examined. Total number 29, as follows: *Benton Co.*: Paterson, 250 ft., 1 (MVZ). *Klickitat Co.*: 1 mi. NE Maryhill, 5 (MVZ); 1 mi. W Lyle, 3 (WWD); White Salmon, 10 (MVZ); 5 mi. W White Salmon, 10 (WWD).

Thomomys talpoides douglasii Richardson

Geomys douglasii Richardson, Fauna Boreali—Americana, Vol. 1, p. 200, 1829.

Geomys fuliginosus Schinz, *Mamm.*, Vol. 2, p. 136, 1845.

Thomomys douglasii Allen, *Bull. Amer. Mus. Nat. Hist.*, Vol. 5, p. 66, August 28, 1893.

Thomomys douglasii douglasii Bailey, *N. Amer. Fauna* 39, p. 116, November 15, 1915.

Thomomys talpoides douglasii Goldman, *Jour. Mamm.*, Vol. 20, p. 235, May 14, 1939.

Type. Obtained near old Fort Vancouver, Clark County, Washington, by David Douglas, probably in 1825, and probably no longer in existence (see Bailey, 1915).

Range. The Pleistocene gravel terraces (locally known as plains) of the Columbia River near Vancouver, Clark County.

Intergradation. None.

Color. Adult topotypes in fresh summer pelgae are between Ochraceous-Tawny and Ochraceous-Orange in color.

Comparisons. *T. t. douglasii* differs from all other gophers in Washington in that the postauricular patches are wanting or small and in that the zygomatic arches are markedly expanded anteriorly.

Specimens examined. Total number 15, as follows: *Clark Co.*: 5 mi. E Vancouver, 13 (WWD); Brush Prairie, 1 (WWD); Orchards, 1 (WWD).

Thomomys talpoides glacialis Dalquest and Scheffer

Thomomys talpoides glacialis Dalquest and Scheffer, *Proc. Biol. Soc. Wash.*, Vol. 55, p. 97, August 13, 1942.

Type. Adult male, skin and skull, No. 272033, U. S. Nat. Mus., Biol. Surv. Coll., obtained 2 mi. S Roy, Pierce County, Washington, by W. W. Dalquest, December 19, 1941; original No. 2672.

Range. Known only from the prairies south of Roy, Pierce County, Washington.

Intergradation. None known.

Color. Specimens in fresh winter pelage are nearest to Cinnamon.

Comparisons. Compared with *tacomensis*, *glacialis* is paler and more yellowish. The underparts of *glacialis* are distinctly more ochraceous than those of *tumuli*, *pugetensis*, or *yelmensis*. The skull of *glacialis* is relatively shorter and wider with more flaring zygomatic arches than those of other races from the Puget Sound area.

Specimens examined. Total number 50, all from the type locality (BSC).

Thomomys talpoides tacomensis Taylor

Thomomys douglasii tacomensis Taylor, *Proc. Biol. Soc. Wash.*, Vol. 32, p. 169, 1919.

Thomomys talpoides tacomensis Goldman, *Jour. Mamm.*, Vol. 20, p. 235, September 30, 1919.

Type. Young adult female, No. 231196 U. S. Nat. Mus., Biol. Surv. Coll., obtained 6 mi. S Tacoma, Pierce County, Washington, by G. G. Cantwell, December 24, 1918; original No. 857.

Range. Seemingly restricted to certain prairies near Steilacoom and prairies and some agricultural lands near Tacoma; all in Pierce County.

Intergradation. None known.

Color. Adult topotypes in fresh winter pelage are nearest to Hazel in color, but are brighter.

Comparisons. The especially rich hazel color of *tacomensis* distinguishes it from all gophers found about Puget Sound, save *couchi*, from which *tacomensis* differs in much larger size and in cranial characters (see Fig. 8).

Remarks. As far as we could discover, there are no gophers on the extensive prairies of the Fort Lewis area, between the ranges of *tacomensis* and *glacialis.* Mima mounds occur on the prairies 2 miles south of Spanaway, showing the existence in the past of a geographically connecting population.

Specimens examined. Total number 41, as follows: *Pierce Co.*: Tacoma, 9 (BSC); University Place, Tacoma, 3 (BSC); ½ mi. E Tacoma Narrows, Tacoma, 5 (BSC); 1 mi. S Day Island Bridge, Tacoma, 3 (BSC); 5 mi. SW Tacoma, 21 (BSC 6, WWD 15).

Thomomys talpoides pugetensis Dalquest and Scheffer

Thomomys talpoides pugetensis Dalquest and Scheffer, *Proc. Biol. Soc. Wash.*, Vol. 55, p. 96, August 13, 1942.

Type. Adult male, skin and skull, No. 272032, U. S. Nat. Mus. Biol. Surv. Coll., obtained 4 mi. S Olympia, Thurston County, Washington, by W. W. Dalquest, December 31, 1941; original No. 2022.

Range. Known only from prairies south of Olympia, in Thurston County, Washington.

Intergradation. None known.

Color. Topotypes in fresh winter pelage are nearest to Snuff Brown.

Comparisons. Compared with *tumuli*, *pugetensis* is yellower in color, less grayish, and has a shorter, relatively wider skull. Dark patches on the sides of the neck distinguish *pugetensis* from all other gophers in the Puget Sound area, save *tumuli*.

Specimens examined. Total number 54, all from the type locality (BSC 26, WWD 28).

Thomomys talpoides tumuli Dalquest and Scheffer

Thomomys talpoides tumuli Dalquest and Scheffer, ***Proc. Biol. Soc. Wash.***, Vol. 55, p. 96, August 13, 1942.

Type. Adult male, skin and skull, No. 272034, U. S. Nat. Mus., Biol. Surv. Coll., obtained 7 mi. N Tenino, Thurston County, Washington, by W. W. Dalquest, January 2, 1942; original No. 2781.

Range. Known only from Rocky Prairie, 7 mi. N Tenino, Thurston County, Washington.

Intergradation. None known.

Color. Topotypes in fresh winter pelage are between Cinnamon and Sayal Brown in color.

Comparisons. Compared with *yelmensis*, *tumuli* is larger, darker, and possesses dark patches on the neck.

Specimens examined. Total number 36, all from the type locality (BSC 30, WWD 6).

Thomomys talpoides yelmensis Merriam

Thomomys douglasi yelmensis Merriam, ***Proc. Biol. Soc. Wash.***, Vol. 13, p. 21, Jaunary 31, 1899.

Thomomys douglasii yelmensis Taylor, ***Proc. Biol. Soc. Wash.***, Vol. 32, p. 169, September 30, 1919.

Thomomys talpoides yelmensis Goldman, ***Jour. Mamm.***, Vol. 20, p. 243, May 14, 1939.

Type. Adult male, No. 31916, U. S. Nat. Mus., Biol. Surv. Coll., obtained at Tenino, Thurston County, Washington, by C. P. Streator, October 24, 1891; original No. 1385.

Range. Grand Mound Prairie, near Tenino; Vail Prairie, near Vail; Rochester Prairie, near Rochester; all in Thurston County, Washington.

The original type locality was given by Merriam, (*loc. cit.*) as "Tenino, Yelm Prairie." At the present time the prairie at Tenino is known as Grand Mound Prairie. A prairie now known as Yelm Prairie is situated 13 mi. NE Tenino, and, as far as could be ascertained, no gophers exist there.

Intergradation. None known.

Color. Adult topotypes in fresh winter pelage are between Tawny-Olive and Sayal Brown in color.

Comparisons. This race differs from *couchi* in larger size and yellower, duller color.

Specimens examined. Total number 147, as follows: *Thurston Co.*: 1 mi. S Tenino, 63 (BSC 17, WWD 34, MVZ 12); 2 mi. N. Rochester, 50 (BSC); 1 mi. W Vail, 34 (BSC, 30, WWD 4).

Thomomys talpoides couchi Goldman

Thomomys talpoides couchi Goldman, *Jour. Mamm.*, Vol. 20, p. 243, May 14, 1939; Hall and Dalquest, *Murrelet*, Vol. 20, p. 38, August 10, 1939.

Type. Adult male, skin and skull No. 243092, U. S. Nat. Mus., Biol. Surv. Coll., obtained at Scotts Prairie, 4 mi. N Shelton, Mason County, Washington, by L. K. Couch; X-catalog No. 22896.

Range. Isolated prairies at the southeastern base of the Olympic Mountains; recorded from Scotts Prairie and Lost Lake Prairie, Mason County.

Intergradation. None known.

Color. Adult topotypes in fresh winter pelage are nearest to Hazel in color, but are brighter.

Comparisons. The rich hazel color of *couchi* distinguishes it from all other subspecies of gophers found in the Puget Sound area, save *tacomensis,* from which it differs in much smaller size.

Specimens examined. Total number 55, as follows: *Mason Co.*: 4 mi. N Shelton, 48 (BSC, 18, WWD 27, MVZ 3); Lost Lake Prairie, 7 (WWD).

Thomomys talpoides melanops Merriam

Thomomys melanops Merriam, *Proc. Biol. Soc. Wash.*, Vol. 13, p. 21, January 12, 1899.

Thomomys douglasii melanops Bailey, *N. Amer. Fauna* 39, p. 119, November 15, 1915.

Thomomys talpoides melanops Goldman, *Jour. Mamm.*, Vol. 20, p. 235, May 14, 1939.

Type. Adult female No. 90630, U. S. Nat. Mus., Biol. Surv. Coll., obtained at timberline at head of Soleduck River, Clallam County, Washington, by V. Bailey, August 28, 1897; original No. 6219.

Range. Alpine meadows of the high Olympic Mountains.

Intergradation. None known.

Color. An adult in slightly worn summer pelage is nearest to Tawny-Olive in color, but is duller.

Comparisons. Compared with *couchi, melanops* is larger, duller, and much grayer. Compared with *yelmensis, melanops* is duller, grayer, and has more black on the sides of the face. Compared with *shawi, melanops* possesses larger postauricular patches and much more black on the sides of the head.

Specimens examined. Total number 8, as follows: *Clallam Co.*: Timberline at head of Soleduck River, 2 (BSC); Cat Creek, 4500 ft., 2 (BSC); Happy Lake Ridge, 1 (BSC); Canyon Creek Divide, at head of Bogachiel River, 3, not typical (CRC).

SUMMARY

The descent of the Vashon-Wisconsin continental glacier eliminated all pocket gophers north of the drift border in the state of Washington. At the maximum extent of the ice sheet, gophers were present in the southern Cascade Mountains, on the Columbian Plateau, and in southeastern Washington. The dark-colored gophers of southeastern Washington were connected to those of the southern Cascade Mountains by a humid "bridge" along the Simcoe Anticline. This bridge, which was occupied by dark-colored gophers, isolated the pale gophers of the Columbian Plateau. With the retreat of the glaciers the Simcoe Bridge became more arid and no longer served as a geographically continuous habitat to connect the two dark-colored populations. The pale gophers of the Columbian Plateau then extended their range south, along the valley of the Columbia River. Gophers from Idaho invaded the land north of the drift border, recently cleared of ice, and extended their range to the west and south until they nearly encircled the pale gophers on the Columbian Plateau. The dark gophers of the southern Cascades pushed their range westward, on glacial outwash trains, to the glacial prairies of the Puget Sound area, the Olympic Mountains, and to river-terrace prairies in southwestern Washington.

The fossorial habits of pocket gophers, their limited tolerance with regard to ecologic conditions, and their ability to exist for long periods of time in a single locality, all combine to make gophers subject to isolation by barriers that ordinarily do not restrict the movements of other vertebrates. As one result, pocket gophers within areas circumscribed by the more rigid barriers exist as independent populations in areas suitable to their needs. Such isolated populations behave as small, independent units and, as a result of different selective factors and the chance fluctuations of genetic factors, develop into microgeographic races. As a whole, the barriers separating these microgeographic races are constantly breaking down and reforming. Thus, isolation and intermingling of populations are constantly going on. Characters developed in microgeographic races might eventually spread throughout a subspecies as a result of successive chance ''conquests'' of other small populations or as a result of natural selection.

Color was studied in the seventeen races of gophers from the entire state of Washington. Differences in the color of the various races were found to be due principally to variations in the amount or kind of pigment present throughout the entire length of each hair. The variations in the amount or kind of this pigment are thought to be due to chance combinations of alleles of a multiple factor series. The gross color is modified by the relative length of the sepia-colored proximal band of the fur.

As a result of our now clearer understanding of the immigrational history and microgeographic variation of the pocket gophers of Washington, and in the light of our tentative genetic analysis of the variations in size, color and skull, we conclude that seventeen subspecies, all belonging to the species *Thomomys talpoides,* occur in the state.

Eight isolated populations of pocket gophers in the Puget Sound area, belonging to five subspecies, came from a common stock in post-Pleistocene times and now occupy similar but isolated habitats. Large samples of these populations were collected and studied in an effort to correlate differences in their habitats. Quantitative differences in size and cranial construction were found to be correlated with the depth of the soil in the habitat occupied. Depth of soil seems to act as a selective factor in the fixation or loss of genetic factors, already present or newly acquired, in a multiple factor series for size. No correlation between the color of the gophers of the Puget Sound area and any measurable feature of their environments was found. It is concluded that selective factors for color are less strong than those for size and quantitative cranial characters.

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FISHES THAT PLAY "LEAPFROG"

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FISHES are given to leaping for many reasons: in fear or panic, to escape their enemies, to ascend waterfalls, to capture food and sometimes in sheer exuberance of spirits—in plain English, in fun or play. But the allegation set out in the title is so very extraordinary that the reader has already ejaculated—"Preposterous!" Maybe, but let us consider the evidence.

ORDINARY LEAPFROGGING

When boys play ordinary leapfrog, one called the "back" stands firmly with back to the leaper, with hands on knees and head bowed. The leaper takes a short run to the "back," places his hands on the other's shoulders and with wide-forked legs lifts his body head up (vaults) over the "back." The evidence that fishes likewise vault over sticks, bits of grass, a turtle or another fish will now be presented.

THE SALTWATER GARS—FAMILY BELONIDAE

These sharp-nosed marine gars are nearly all leapers and many accidents to fishermen have resulted from this habit. But before we consider the earliest record of the leapfrog habit in the young of these fishes, a biographical note is in order with reference to the man who made this record and to the locality where it and other observations have been made.

C. F. Holder spent a good part of his most impressionable years (11–18) at the Dry Tortugas, Florida, those last farflung outliers of the great Florida Reef. Here his father, Dr. J. B. Holder, was surgeon and health officer to the Federal Military Prison on Garden Key from 1862 to 1869. The son's life during these years seems mostly to have been spent on the reefs and the channels in between. As an outcome of his many adventures at the

Tortugas, he has written a series of most interesting books dealing with the fishes of the Florida Reef.

In an early book (1892) he gives the first account so far found of this interesting leapfrog habit of fishes. It reads as follows:

> "Keep still!" whispered Long John [the fishing mentor of the boys at Tortugas in the early days]. "Keep still, and you'll see a game of leapfrog."
>
> And surely enough they did, but the "frogs" were a turtle and the fish. The hawksbill was floating with its back several inches out of water, when suddenly a garfish leaped completely over it. Another made the attempt, half-turning in the air, two more followed suit—one turning a somersault—while still another, not quite so dexterous, failed in his act of lofty tumbling, and landed plump on the turtle's broad back, startling it so that it dived out of sight.
>
> "I didn't know that fishes played games before," remarked Harry.
>
> "They do, though," replied Long John; "and, as for these fellows, they give that poor turtle no peace. The minute he comes to the surface they begin their tricks, and if they can't jump over him they find some floating stick or straw and practice on that!"

Holder's account is illustrated by the accompanying drawing (Fig. 1), the only portrayal of this habit known to me. If only there were photographs or a motion picture film of this interesting performance.

In a later book (1899) Holder again writes of these leapfrogging fishes at Tortugas as follows in a section entitled "The Games of Animals":

> Fishes have a decided sense of humor, judging from certain exhibitions that have been observed; the young especially have numerous games or methods of amusement; and their mischievous natures can best be appreciated when a large school is under observation. Through the flooring of a wharf in tropical waters at Fort Jefferson, Tortugas, I have often watched the varied throngs unsuspected and unseen. Such games and sports as they indulge in! Now a floating straw is discovered on the surface, and over it with a daring leap the leader goes, followed by the rest, until the leapers in a continuous glistening stream dart into the air.
>
> The game of leaping over various objects, I have noticed in many fishes, especially in the young garfish; and in an aquarium built out into the water at Garden Key I have frequently seen them leaping over a hawksbill turtle that floated on the surface. This game at the expense of the turtle was kept up for some time, until a garfish in leaping landed fairly on the sleeper's back, when the astonished and indignant turtle took a long breath and dashed away, scattering the assembled fishes far and wide.

Fifty years (1912–1915) after Holder, I realized a lifelong ambition by going to Tortugas to study its fishes—at the Marine Biological Laboratory of the Carnegie Institution of Washington with that prince of directors, Alfred Goldsborough Mayor, in charge.

On the floor of that wharf (renewed many times since Holder's day) I laid down time after time and through the cracks watched the fishes. But never once, to my keen disappointment, did I see the leapfrog game. However, this game had not been discontinued, and other men have later been more fortunate.

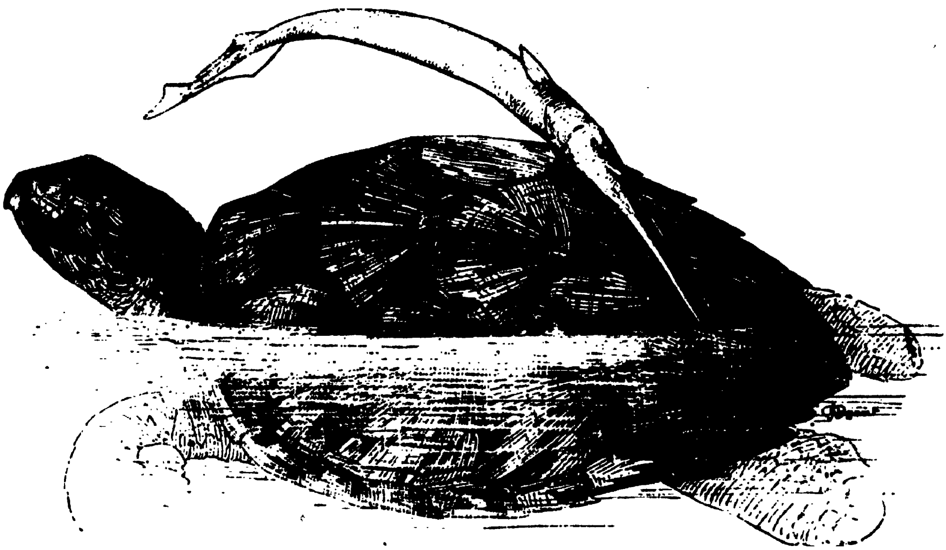

FIG. 1. A marine garfish (family Belonidae) leaping over a sleeping turtle at Fort Jefferson, Garden Key, Dry Tortugas.

Strongylura (*Tylosurus*) is the genus of the Belonidae (needlefishes) to which all the identified leapers at Tortugas belong. Holder unfortunately did not give the scientific name of his fish, but, as Fig. 1 shows, it is surely a needlefish. It is now known that three species of Strongylura there practice leapfrogging—*ardeola, raphidoma* and *notatus*—named in the order of their addiction to this interesting practice. The ascertained facts of the leaping of these fishes will now be given.

Following some 60 years after Holder, W. H. Longley (with whom I worked in the laboratory on Loggerhead Key during the summers of 1913–1915) made the next observations of the leaping gars at Tortugas. Hildebrand, who after Longley's death in 1937 wrote the report on Tortugas fishes (1941) from Longley's incomplete MS. and fragmentary notes, thus quotes him on the behavior of *Strongylura raphidoma:*

> At the dock I noticed *S. raphidoma* giving an exhibition of its interesting play. Five or six specimens were jumping over a piece of floating paper. Sometimes one would go back and forth quickly as many as three times. Sometimes one would put its snout slowly above the paper and then quickly glide across it; more usually they would make a clear leap. One caught its beak in the water after leaping and turned a somersault (apparently accidentally). This morning [July 9, 1923], the fish were jumping across a floating feather, and two larger fish were jumping across the floating body of a fish of their own species.

In 1929, C. M. Breder studied fishes at the Tortugas Laboratory and made more extensive observations than any one else has ever done on the leapfrog habit of the fishes of the family Belonidae. Of his studies he made a preliminary report later in the year.

When he described this interesting procedure, he did not know of Longley's observations, which were made earlier but were not published until four years after his untimely death in 1937. Thus Breder's careful studies, though made later, were published earlier (1929). Here is what he saw and recorded in two articles.

> Observations were made on the habit of fishes of the genus *Strongylura* of vaulting over small floating twigs, straws, etc. *S. ardeola* seems most addicted to the practice, with *S. raphidoma* and *S. notatus* following in the order named. Sometimes a single fish would leap back and forth as many as a dozen times over a single straw. It is thought that the function of this well-marked habit is that of scratching to remove ectoparasites, for it was noted that usually some part of the fish was rubbed against the straw in passing. Second leaps were most often noted when this did not succeed. It is noted in this connection that *S. ardeola,* which was most given to the habit, also most frequently harbored ectoparasites, such as argulids, etc. These fishes, living almost entirely at the surface, do not have rocks for purposes of scratching, such as do bottom fishes, and it is inferred that they make use of what floating objects they may for such purposes; this apparently playful act seeming to have a very practical function.

In a fuller report (1932) of his Tortugas studies, Breder writes in more detail of this habit in fishes of the family Belonidae as follows:

> With a shoal of such fishes of a dozen or more, the throwing of a small splint or straw in their midst will, in the writer's experience, invariably cause at least one to leap over it. Usually several will leap and sometimes a single individual will vault back and forth repeatedly. In carrying out such experiments, small sticks about ⅛ inch square and from 4 to 12 inches long were offered to fishes from 12 to 16 inches long. A few statistical comments were made as follows:

Length of stick	*Length of fish*	*No. of fish leaping*	*No. of leaps*
4 inches	12 inches	2	1 each
12	14	1	1 (Tried 3 times before success)
8	12	4	1 each
8	12	1	9 times back and forth
6-inch piece of *Cymodocea*	12	1	3 times back and forth

> This gives a fair idea of the reactions of a small school of these fishes to such floating objects before they drift out of the range of the school proper. An interested fish will seldom go very far from his school in following such a floating stick for purposes of leaping.
>
> The actual action in leaping is most often as follows: First the fish will swim up slowly to the stick so as to be nearly at right angles to it (in a horizontal plane) and gently protrude the beak through the surface of the water, sliding the tip over the stick. Usually if the stick is too small and gives way too easily, or too large and gives way too little, the fish will withdraw. If it is of the proper buoyancy and sinks ever so little under the weight of the beak, a violent tail action follows and the fish clears the water, but in such a manner that usually part of the body rubs against the stick in passing and the fish falls to the other side, from which it may turn and leap back again.
>
> *Tylosurus raphidoma* uses much more physical effort to accomplish this performance and is less inclined to show interest in such floating objects.

Then he repeats his argument, set out in Year Book No. 28 and quoted above (1929), that this action is for the purpose of ridding the fish of external parasites, and concludes thus: "This species, *T. raphidoma,* was commonly parasitized by some hirundid (?). A few were commonly seen on young *raphidoma.* In all cases, however, they dropped off on capture"—from which one gets an idea as to the ease with which they can be scraped off when the leaper rubs against the stick.

As the quotations all show, Breder has gone at the study of this behavior in thoroughly scientific fashion, and made it clear that in his leapers the action is purposive—the scraping off of parasites.

THE HERRING, CLUPEA HARENGUS, ALSO PLAYS LEAPFROG

In 1931, Breder (1932) was fortunate in seeing this fish also play leapfrog off Block Island, northeast of Montauk Point, Long Island. Here is his account of its action.

> On July 10, 1931, specimens about three inches long in large schools were observed to leap over broken fragments of *Zostera* in a manner similar to that described for various Belonidae at the Dry Tortugas. . . . The action was clearly similar, although more frequently specimens were noted to scratch themselves on entirely submerged fragments. This behavior on the part of three clupeids seems to be quite intermediate between the specialized scratching activities of belonids and the more generalized performances of various bottom fishes.

LEAPING BY A SARDINE

Earlier in this article, Holder is quoted that he has noticed this behavior in "many fishes," but he does not name them. In a later and general article (1913) on leaping by fishes, he repeats the statement about the gars leaping over the turtle and then adds "I also observed [at Tortugas?] small sardines leap over a floating twig." But he gives neither details nor the scientific name of the fish, and the name sardine in colloquial usage may mean any small fish.

ATHERINA HARRINGTONENSIS, A LEAPER AT BERMUDA

William Beebe thus describes (1932) the behavior of these little fish at Bermuda:

> With a quiet school of Silversides and a wooden match . . ., I can magic play out of the usually serious, preoccupied little fish. A sinking pebble bores through a school of these . . . but a small splinter of wood or match thrown on the surface above the school has almost no effect. A few, directly beneath, may flinch slightly, but after a minute one, two, several, will drift up to the bit of wood and begin to leap over it. First one, then another goes over the hurdle, from this side or that, sometimes balking at the start and swimming away, more often flinching sideways, a leap clear of the surface, but very unlike the high, forward course when fleeing for life from an impi [army] of mackerel. This may accomplish some real purpose, either practice or achievement, to which we have no clue, but as far as appearances go, it is sheer exuberance.

John Tee-Van states (in a personal communication) that, while working at Bermuda with William Beebe in 1929–1931, he has at various places and times seen Atherinas (generally only one or two) play the leapfrog game. They vaulted over matchsticks or bits of straw on days when the water was calm, and in each case the leaping was continued for awhile as if the fish were enjoying itself. Their vaulting did not differ from the performance recorded by Beebe.

Apparently this playing leapfrog by small fishes at Bermuda is no new thing. Mr. Hawthorne Daniel, formerly editor of *Natural History* in the American Museum, told me some years ago that in November, 1927, he saw a little fish so performing in the channel off the Aquarium at Flatts. From a school of small fishes in the channel, one detached itself and, finding a floating twig a little distance away, played its game all by itself. It would swim up to the twig and push it with his nose. Then it would back off a short distance, and take a run to and leap over the twig. Then instead of leaping back, it would swim under the twig to the starting point, and repeat the performance. This was done a number of times. Mr. Daniel did not know what the fish was. Probably it also was *Atherina harringtonensis.*

ATHERINA ARAEA OF HAITI A LEAPFROGGER

John Tee-Van states that, in 1927, while studying fishes in Port-au-Prince Bay, he observed Atherinas of this species leaping over sticks and straws. Generally the leaping was done by a single fish or at most by two, and on quiet days. "There was very little control by the fish of its movements when it was in the air. It either leaped over the stick and dived into the water head first, or landed on its side, but apparently without injury since the distance was small. This performance was repeated, as if the little fish found it enjoyable."

This leaping by these Atherinas singly is interesting, since these small fishes are usually found in schools.

And now to be recorded are unpublished first-hand accounts of observations on the leaping habit made in the vicinity of New York by two men in the American Museum. Both are anglers and as such have frequently observed leapfrogging fishes. These observations they have kindly reported for inclusion in this article.

The Silverside, Menidia notata, Also a Leapfrogger

Louis Monaco has seen this behavior in these little fish in Sheepshead Bay on the southeastern ocean side of Long Island. Usually during September the waters are alive with these small fish, locally called "fish bait" or "spearing"; and here is what they do:

> Year after year, while fishing for snappers and using a cork bob, I have watched with amusement and fascination the antics of these little fish. The fishing line attached to the top of the cork or bob forms a little loop which rises above the surface of the water when the line is slowly drawn in, or sinks slightly under the surface when the line is let out. As long as the water is quiet and not disturbed by passing boats, these fish seem to have a lot of fun leaping over this loop. They leap out of the water and over the line whether the line is slightly under the surface or on the surface and will make a high-jump over it if the line is above the surface. The fascinating part of their leaps over the line, when it is above the surface, is whether or not they will make it. Most of the time they hit the line and bounce back, not having cleared it. Their leaps are not graceful and they often turn over in the air, land sideways, or tail first instead of head first. I have seen them do the same thing over a matchstick thrown in the water. In either case so many follow in succession at times that it seems to be a game of "follow the leader."

John Germann has seen like behavior of these same "spearing" and here is his description of it:

> While sailing on Long Island Sound, I have often been entertained by the sight of "spearing" leaping back and forth over floating stalks of grass, and over bits of driftwood from the size of a lath to that of a broom handle. The number of leapers varies from one or two to a small school of possibly six or eight. They leap over, turn around and leap back, seemingly in play, or in the indulgence of an acrobatic sport. This habit is so well established, that (especially with guests aboard) I always steer for any small floating objects, since the fishes are sure to leap and the sight never fails to please.

This concludes all the accounts (published and verbal) that I have come upon of ordinary leapfrogging by fishes.

But there are now to be recorded instances of a much more unusual type of such action. These are brought together in a section bearing the title:

FISHES THAT PLAY SOMERSAULT LEAPFROG

This is another form—a variant—of the leapfrog game with boys. The "back" is always a stout fellow chosen to withstand shock and weight. The "back" plants himself solidly with hands on knees and head bowed. The runner takes a short start, and when he approaches the "back" places his hands on the latter's hips, throws his feet up in the air, rests his head on the "back's" shoulders, turns a somersault heels-over-head, alights on his feet and after a short run recovers himself. This calls not only for more strength and agility but also for more judgment and coordination than does the ordinary leapfrog game. That fishes also do the somersault or tail-over-head leapfrog act is as new to the present writer (who for years has been collecting accounts of the ordinary kind) as it is to the readers of this article.

Holder in his first acount of the fish vaulting over the turtle says that one turned a somersault, but does not explain. However, Longley does, for he says that "One *Strongylura raphidoma* caught its beak in the water after leaping and turned a somersault (apparently accidentally)."

Fortunately, there came, at this point in these studies, a letter from Mr. Louis S. Mowbray, director of the Bermuda Aquarium, describing how three kinds of fishes in the waters around those islands continually and normally do the somersaulting leapfrog act. The information he gives is based on personal observations extending over a period of years on performances of "at least several hundred times." This action of these three fishes was always noted "when the water was quite smooth though not necessarily in a flat calm." The first of these fishes are those which also play the simple game of leapfrog as described above. This is a very interesting point.

THE SOMERSAULTING ATHERINA HARRINGTONENSIS AT BERMUDA

Of these Mowbray writes as follows:

> The sight of this Atherina "flipping" is very common around harbors. The fish shows a preference for wooden match sticks, while in other places it will be a thin twig or single blade of grass.
>
> The action is thus performed. The little fish approaches slowly and pushes the chin of the lower jaw against the object and with a quick flip of the tail, aided no doubt by the pectorals and ventrals, it leaves the water tail first and completes a somersault tail-over-head over the floating object landing almost invariably on its side and facing at a right angle to its former direction. The greatest number of consecutive flips that I have ever observed of a single Atherina was 9. This was done over a matchstick in Harrington Sound, and was observed at a distance of about 25 feet. But as the maximum length of Atherina is slightly under 3 inches, it was impossible to determine whether this act was done to remove a common louse-like parasite or for play. I really believe that it was a combination of both.

"FLIPPING" OF TWO HEMIRAMPHID OR HALF-BEAK FISHES

These fishes are close relatives of the Belonidae, and being leapers it is not surprising that they also play leap-frog. But it is rather surprising that they play the somersaulting instead of the vaulting game of their cousins, the Belonids, at Tortugas.

Hemiramphus brasiliensis, the balao, has been seen in the "flipping" act many times by Mr. Mowbray. Here is what the fish does:

> The balao will approach and inspect some small floating object, such as a match box, or a thin flat piece off a wooden box, or a large single "leaf" of a seaweed which has floated to the surface. Then he will put the tip of his long lower jaw under the object and at the same time give a flip which almost invariably lands him tail first on the other side of the object and on his side generally but facing the opposite direction. This may be repeated five or six times within twenty seconds. Once I saw three fish of this species performing at one time on a single piece of box wood about 15 inches long. This was in Harrington Sound, behind the Bermuda Aquarium. It was the only time that I had seen more than one fish flipping at one time, so I recorded it then and there.
>
> *Hyporhamphus unifasciatus,* another half-beak, performs similarly, but since it is not so common as the other two fishes in my fishing areas, I have made no special observations on it, though the performance shows no apparent difference from that of the other fishes. I have never seen one of these fish land head first—except when it was very obviously an accident due to a poor

flip. *H. unifasciatus* is a small fish only about five inches long while the balaos average 10 to 12 inches in length.

Given herein are accounts by 7 observers of ordinary leapfrogging by 7 species of identified and 2 of unidentified fishes in such widely separated regions as Block Island, Long Island (both shores), Bermuda (various localities), Tortugas and Port-au-Prince Bay, Haiti. In addition there are accounts by one scientific man ("based on hundreds of observations") of somersault leapfrogging by 3 species of fishes in Bermuda. These multiplied observations in these widely separated localities lead inevitably to the conclusion that this curious action is by no means of infrequent occurrence. However, these are all the accounts, published and verbal of this curious behavior in fishes that have come to light in the course of this study. Probably other such observations are buried in books and systematic articles or indeed have been made but never published. It is hoped that the gathering and publishing of the above accounts may lead others to watch for and bring to light their observations of this curious behavior in these and other fishes.

HOW AND WHY HAS THIS LEAPFROG HABIT ARISEN?

Two answers have been suggested. But, as noted, Breder is the first to suggest an answer based on careful scientific studies. From close observation of the leaping garfishes at Tortugas, he found the most common leaper, *Strongylura ardeola,* to be infested with ectoparasites, and that in leaping most generally some part of its body scraped the stick. His observations surely establish the fact that his little gars were trying to free themselves from external parasites. But his report of the leaping of small clupeids off Block Island is by no means so conclusive. One other man only has suggested the freeing of the fish from parasites. Mowbray notes that *Atherina harringtonensis,* a leaper at Bermuda, harbors ectoparasites. But he was not able to say whether the leaping was to scrape off such or in play. Indeed he thought that it possibly partook of both purposes. Then the question comes—"Do all leapfroggers leap to get rid of parasites?"

C. F. Holder, at Tortugas sixty or more years before Breder, was convinced that the fishes were doing this in play. Certainly there was no scraping when the gars leaped over the sleeping turtle—for at the first touch it awoke and dived. Moreover, Holder's little gars followed their leader over the straw "in a continuous glistening stream."

In Holder's latest article (1913), bearing the title "How and Why Fishes Leap?," I have looked in vain for evidence of rubbing off of parasites. However, this is a general article on leaping by various fishes for various reasons. Of the leapfroggers, he reiterates that, so far as he could discover, their leaping was, like that of children over an obstacle, done in fun.

Furthermore Longley's gars leaped over a piece of floating paper, a feather, and "two larger fish were jumping across the floating body of a fish of their own species." Apparently these fish did not touch the objects over which they leaped, and no "scratching" was observed.

At Bermuda, Beebe concluded that the little Atherinas were leaping in "sheer exuberance." Tee-Van states that both at Bermuda and Haiti the Atherinas "leaped as if they found it enjoyable." And at Bermuda, Daniel's little fish certainly played a game, while Mowbray has seen an Atherina leap as many as 9 times consecutively, and a Balao leap 5 or 6 times in 20 seconds. Furthermore, he has seen three of these fish leap at one time over a 15-inch strip of wood.

Monaco's observations of silversides in Great South Bay near New York City indicate plainly that, with these little fish, the leaping over the fisherman's line in close succession is purely a matter of sport—no "scratching" was observed. This is confirmed by Germann's account.

Among Breder's young gars, a "single individual would vault back and forth repeatedly''—in one case as many as nine times. To me this savors of play as well as of possible utility.

It is well known that the young (and even adults) of the higher animals (mammals especially) are given to play. One need not labor the point, but all know of the play of wild mammals; otters young and old play on their toboggan slides, and fawns and young foxes chase each other in fun. Birds likewise have their games. In short the play instinct seems fundamental—certainly in the higher animals.

To me it appears that what seems to be primarily a sport in these leapfrogging fishes has in certain ones assumed a utilitarian function. At any rate both things seem to be factors in this very curious habit. More and more widely diversified observations are needed, and snapshot photographs are special desiderata.

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REVIEWS AND COMMENTS

EDITED BY DR. CARL L. HUBBS

IN these section reviews and notices of current publications on general biology emphasis is given to books and major articles which fall within the special scope of THE AMERICAN NATURALIST, in that they deal with the factors of organic evolution. REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

The Woods Hole Marine Biological Laboratory. By FRANK R. LILLIE. Chicago: University of Chicago Press, 1944: i–ix, 1–284, 28 figs. $4.00.

AIDED by E. G. CONKLIN, with whom joint authorship was originally planned, Frank Lillie presents a detailed and well-documented, yet fascinating history of the Marine Biological Laboratory, with briefer accounts of the sister laboratories at Woods Hole—those of the United States Fish Commission (successively the Bureau of Fisheries and the Fish and Wildlife Service) and the Oceanographic Institution. A background on the geography and early history of Woods Hole is first presented by Conklin. Then Lillie proceeds with a significant chapter on the origin of marine laboratories, including the dramatic story of Louis Agassiz at Penikese. Conklin recounts the establishment of the Fish Commission Laboratory and Lillie treats Alpheus Hyatt's seaside laboratory at Annisquam, which was most directly ancestral to the Marine Biological Laboratory. The relation of some good ladies of Boston to the Annisquam project and to the embryonic Woods Hole station is made clear: "The first step in the foundation of the Marine Biological Laboratory was taken by the Woman's Education Association in accordance with their decision to replace the Annisquam Laboratory by an independent and permanent station." Their generosity and far-sightedness is duly acknowledged, though it led to the domination of the first Board of Trustees by a group of Bostonians whose limited geographic view and rigid New England economy came into sharp conflict with the broad and wise plans envisioned with apparent lack of practicality by the first director, C. O. Whitman. After a trying struggle, the administration of the laboratory was placed under the control of trustees elected by the corporation, which is made up of working biologists from various institutions over the country. Other crises were met, until the nation-wide, democratic organization became a set tradition.

The material growth of the laboratory into the world's greatest center of biological research is treated at length and in detail, fortunately by the man who long guided its development. The almost endless generosity of Charles R. Crane is of course extolled. The magnificent research record is summarized for the first twenty years only, but the dominating position of Woods Hole in the development of biology is amply indicated.

Brief but vivid pen sketches are given by Conklin and by Lillie of four of the dominating personalities of Woods Hole: Whitman, Crane, Drew and Gardiner. The two authors then let us feel the deep influence that the Woods Hole community life has had on the lives of the biologists and their families. Finally, a particularly valuable account is given of the foundation and functioning of the great Woods Hole Oceanographic Institution.

The unbounded enthusiasm and the warranted pride of the authors in the Marine Biological Laboratory left no room for qualifications. They say nothing of the relatively depauperate fauna of the North Atlantic; nothing of the restricted development of biology at Woods Hole, with increasing neglect of morphology, systematics, speciation, evolution, ecology, parasitology, fishery biology, and of many other still active branches of biology that do not emphasize the biochemical and biophysical aspects of the science; nothing of the narrowed view of biology which has thereby become installed in the minds of some scientists trained at Woods Hole. They say nothing of the limitations inherent in greatness, such as the inability of newcomers to gain intimate contact with the masters; almost nothing of policies that have become fixed with age, for example, the limitation of instruction to four traditional courses; nothing of the failure of some Woods Hole habitués to make full use of research opportunities. Might not these limitations be recognized, without detracting greatly from our appreciation of the dominating role that this grand institution has continued to play in biological training and research? Perhaps a fresh consideration of these limitations might lead to even greater and broader progress.

The Skull of Sinanthropus pekinensis; a Comparative Study on a Primitive Hominid Skull. By FRANZ WEIDENREICH. Pehpei, Chungking: Geological Survey of China; New York: G. E. Stechert and Co. Paleontologia Sinica (New Ser. D) 10 (127), "1943" [1944]: i–xxxi, 1–486, pls. 1–93. $10.00 (paper).

THE discovery by Davidson Black of the very apelike hominid *Sinanthropus pekinensis* in a cave at Choukoutien, China, and the further description and interpretation of this missing link during the past two decades by Franz Weidenreich have been outstanding events in what may come to be known as the golden age of paleoanthropology. The extreme detail with which the relatively abundant remains of the "Peking Man" have been described and figured by Weidenreich in this and in preceding treatises should forestall such wasteful controversies as those that raged over the very similar *Pithecanthropus erectus,* largely as the result of the long-delayed and incomplete descriptions by Dubois. Whether or not other authorities will agree with Weidenreich in interpretations, they will all have full factual information.

Varied opinions on the phyletic position and nomenclature of this new fossil man have indeed already been expressed by experts. Some place it very low, others somewhat higher in the direct line of human ancestry, whereas still others regard it as an offshoot from some primitive type. Some regard it as generically distinct from *Pithecanthropus* (the lack of the maxillary diastema may justify this view); others treat the two types as only specifically or even as only subspecifically distinct. All, however, must regard the discovery of *Sinanthropus* and the subsequent researches by Weidenreich as of paramount importance.

This last and most important publication on *Sinanthropus* is more than a very detailed osteological monograph—though that in the end may prove to be its most valuable feature. It includes an extensive comparison between the better known fossil types of man and a general discussion of their phylogeny.

The phylogeny of man is pictured as a very definite rectilinear sequence of stages which have evolved independently in different regions, as in China, the Indo-Australian Archipelago, Europe and Africa. Among known forms *Sinanthropus* and *Pithecanthropus* are regarded as nearest the anthropoid base of this hominid series, and the Neanderthalians are treated as transitional stages, along the several separate lines, between such ancestral types on the bottom and *Homo sapiens* on top. The evolution of man is held to have been a continuous process (or, rather, a completely parallel series of changes), wholly devoid of "chance variation" and of "real discontinuities." The calvaria is thought to have progressively lost its "superstructures" and to have become less massive and more glabellar, in inverse ratio to the degree of reduction of the face. It is admitted that there are some "disharmonies" within the "stages," but the possible association of a *Homo*-like cranium with an anthropoid type of mandible in the Piltdown Man is discarded as an artificial combination, as a chimera, and the association in *Pithecanthropus* of a *Sinanthropus*-like skull with a curved femur is held to be unacceptable. From the viewpoint of the principles of phylogeny, however, I see nothing unexpected or incongruous in such major differential combinations of archaic and progressive features. Varied associations of characters seem to be the rule in involved phylogenies, particularly in those that have been complicated by reticulate evolution, as the human series seems to have been.

The transformation of the skull and face in human evolution is regarded as only a special case of a common evolutionary change. The domelike, thin-walled, brain-filled skull of man is paralleled by similar end structures in dwarf dogs and in the smaller species of various animal types. The concept of fetalization, however, is not mentioned in this connection.

In the scientific naming of the Hominidae Weidenreich violates the International Rules of Zoological Nomenclature as well as good systematic practice. For example, he quotes approvingly his earlier, unjustified renaming of *Homo soloensis* as *Homo primigenius asiaticus,* when he treated this form as a subspecies of Neanderthal man, but he promptly continues to call it *Homo soloensis.* An equally complex violation of the Rules is involved in giving the typical Neanderthal the preoccupied name, *H. p. europaeus. Sinanthropus* is held to represent almost the identical evolutionary stage as *Pithecanthropus,* in fact to be hardly more than racially distinct, yet the name *Sinanthropus* is maintained, because it would have been tactless for Black's successor to have eliminated the name! At least Dr. Weidenreich is frank in his flagrant disregard for the Rules and practices of zoological nomenclature.

The publication of this monumental treatise while the sponsoring nations are at war may receive some criticism at the moment but eventually will become a source of gratification and pride. The candle may be burning low, but it has not been extinguished.

The Mutants of Drosophila melanogaster. By CALVIN B. BRIDGES AND KATHERINE S. BREHME. Publ. Carnegie Inst. Wash., 552, 1944: i–vii, 1–257, pls. 1–3, figs. 1–128. $2.50 (paper), $3.00 (cloth).

THIS dictionary of the genetic structure of the genetically best-known annual species will produce in intermittent Drosophila workers who are not now active with it an acute nostalgia which may easily turn them back to that field. For the constant devotees of Drosophila genetics it will be the ever-ready handbook, never far from the shelves of culture bottles, the binocular microscope and the record book. It puts in concise form, in a single scheme of arrangement, information of a type heretofore available only in scattered form in the seventeen volumes of Drosophila Information Service. The compilation of these data was carried on for many years by Dr. Bridges. Since his death, it has been completed and edited by Miss Brehme, working with Dr. M. Demerec. The important connection of Dr. Bridges with many phases of the evolution of Drosophila genetics is pointed out in a foreword by Professor T. H. Morgan.

The book starts with a short section on symbols of genes and names of characters, including occasional recommendation of one plan when several have been followed, and listing the precautions necessary for accurate crossover data. Then follows the major portion (226 pages) of the work, which is a list of the known mutations in *Drosophila melanogaster*, including many that have been lost or discarded. Information concerning each mutation is given under its symbol, and these are arranged alphabetically. Phenotype names are listed in the same alphabetic order, but the reference there is always to the symbol of the gene. Under this symbol are given the discoverer, date, locus in the chromosomes, references to the literature, a description of the phenotype, the source (whether spontaneous or induced) and other facts which will tell the investigator how useful the gene may be in any particular problem. There are 128 illustrations of mutations in this part.

Twenty-eight wild stocks, most of them still in existence in a few or many laboratories, are listed, with their peculiarities which constitute advantages or disadvantages. The linkage groups, omitting most lethals, are given in the order of their loci, so that one who looks for neighboring genes finds them here, rather than in the alphabetic list. Each group is divided into two parts, one listing the most useful genes, the other those which would be used only in special situations. The small fourth group has a dozen mutations in it. Drawings of the external features of the fly, maps of its salivary gland chromosomes and a list of publications by Dr. Bridges complete the volume.

In its usefulness to a large and widespread group of investigators, this volume is comparable to the international tables in the physical sciences.

A. Franklin Shull

Notices of New Books

Mitosis. By Franz Schrader. Columbia Biological Series, No. 14. New York: Columbia University Press, 1944: i–x, 1–110. $2.00.—In this critical review mitosis, including meiosis, is treated from the physicochemical viewpoint. The whole emphasis is on the explanation of the mechanisms involved in nuclear division. The book is a "survey of past attempts to solve the puzzle that is mitosis. . . . Not one of the many hypotheses that have been broached has in it the definite promise of a final solution. But we have come to realize that mitosis is comprised of a great complex of different mechanisms." That would seem to constitute a good start toward a solution of a problem, the significance of which pervades all branches of biology.

The Peats of New Jersey and Their Utilization. By Selman A. Waksman, H. Schulhoff, C. A. Hickman, T. C. Cordon and S. C. Stevens. Bull. N. J. Agri. Exp. Sta. Rutgers Univ., 55 (pt. B), "1943" [= 1944] : 1–278, pls. 1–15, figs. 1–42.—This thorough, well-illustrated monograph carries much information that will be of value to ecologists and to students of Postglacial changes in floras and climates.

The Pacific World. Edited by Fairfield Osborn. New York: W. W. Norton & Co., 1944: 1–218, 28 maps and figs. $3.00.—Timely and sugar-coated, this little book will no doubt go far toward increasing knowledge of the Pacific half of the world. Stay-at-home Americans as well as many who are now in war service to the westward may learn from its pages essential facts regarding the great ocean, and its weather, islands, peoples and wildlife. The maps are of the pictorial type, and the whole presentation, though authoritative, reminds one of modernized museum exhibits.

Many Happy Days I've Squandered. By ARTHUR LOVERIDGE. New York and London: Harper & Brothers, 1944: i–xi, 1–278, 19 figs. $2.75.—Vivid accounts of a naturalist's adventures in Africa fill this book full of exciting reading. It contains also much first-hand natural history information, particularly on reptiles and mammals.

A New Manual for the Biology Laboratory. By BERNAL R. WEIMER and EARL L. CORE. New York: John Wiley and Sons, 1944: i–vii, 1–213, figs. A–G, 1–156 (many blank). $2.00.—This simplified laboratory guide supplements "Elements of Biology," recently prepared by Strausbaugh and Weimer. It is designed to aid the student in learning biological fundamentals through his own observation. Much of the text consists of thought-provoking questions.

General Zoology. By TRACY I. STORER. New York and London: McGraw-Hill Book Co., 1943 [1944]: i–xii, 1–798, many figs. $3.75.—The fact that this new text has already gone through four impressions attests its well-deserved reception. In the last printing a considerable number of small changes were made, assuring greater accuracy.

AMERICAN SOCIETY OF NATURALISTS

Secretary WILLIAM RANDOLPH TAYLOR announces the following new members of the American Society of Naturalists, elected as of 1943: Charles A. Berger, S.J., William C. Boyd, J. Gordon Carlson, Kenneth W. Cooper, C. W. Cotterman, R. W. Cumley, Lee R. Dice, Orie J. Eigsti, Ugo Fano, Adriance S. Foster, H. Bentley Glass, Myron Gordon, Ladley Husted, John S. Karling, Philip Levine, Walter E. Loomis, Ernst Mayr, Roland K. Meyer, Alfred E. Mirsky, Paul A. Moody, Orlando Park, Arthur W. Pollister, Harold W. Rickett, Herbert P. Riley, George D. Snell, Herman T. Spieth, Herluf H. Strandskov, Eileen Sutton, Johannes Van Overbeek and Alexander S. Wiener.

SHORTER ARTICLES AND DISCUSSION

CORPUS ALLATUM AND CORPUS CARDIACUM IN *CHIRONOMUS SP.*

Histological studies on the endocrine glands of insect larvae have recently been reported from many laboratories. The glandular nature of the Corpus allatum and the Corpus cardiacum is a fairly well-established fact (Wigglesworth, 1934; Burtt, 1937; De Lerma, 1937; Pflugfelder, 1937). But in spite of these works, the histological changes of the above-mentioned endocrine glands during the whole life period of the animal have, so far as the authors are aware, been mostly neglected. The following observation is thus primarily concerned with these changes in the different developmental stages of *Chironomus sp.*

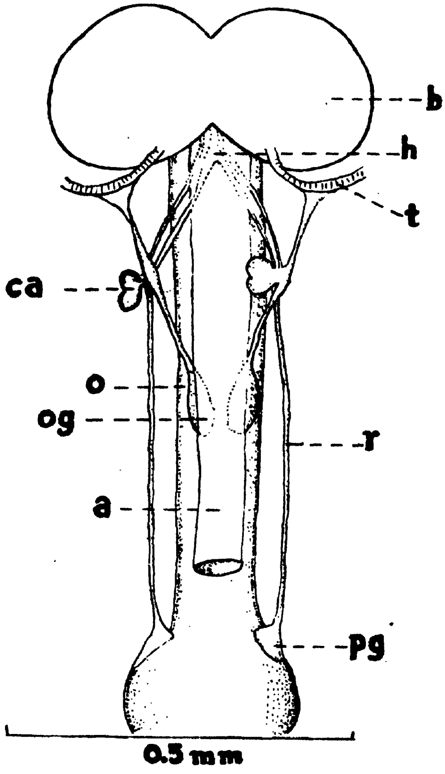


Fig. 1. Corpora allata and stomatogastric system of *Chironomus sp.* reproduced from Burtt. a, aorta; b, brain; ca, Corpus allatum; h, hypocerebral ganglion; o, esophagus; og, oesophageal ganglion; pg, stomachic ganglion; r, recurrent nerve; t, trachea.

Early in 1904, Holmgren recognized that the pair of small round bodies in Chironomus larvae were the Corpora allata, belonging to the stomatogastric nervous system. The system which has recently been studied by Burtt (1937) is reproduced here as Fig. 1. Fig. 2 is a camera lucida drawing from our own prepa-

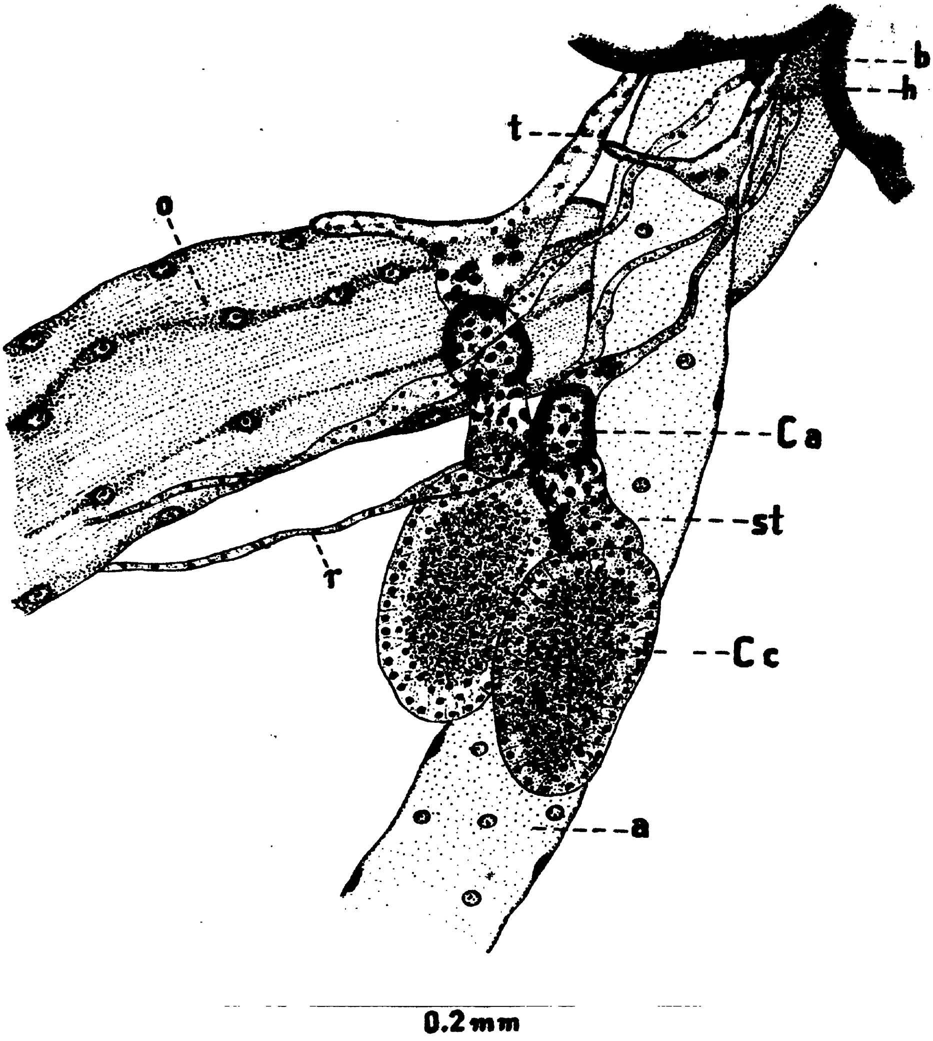


FIG. 2. Corpora allata and Corpora cardiaca of *Chironomus sp.* in last larval instar. In this and the following figures it represents the camera lucida drawing of total mount of the glands; fixed with Bouin and stained with borax-carmine. a, aorta; b, brain; C a, Corpus allatum; C c, Corpus cardiacum; h, hypocerebral ganglion; o, esophagus; r, recurrent nerve; s t, strand tissue; t, trachea.

ration. Despite their general similarity, our findings seem to differ from his in two respects. In the first place, it has been found that the Corpus allatum is imbedded in a strand of tissue which serves as a link between the trachea and the ellipsoid organ, and that they exhibit some conspicuous structural changes in the different developmental stages. Instead of a few cells, each of them is composed of about 25 to 30 cells with nuclei of varying size in the last larval instar. Although there has been little doubt as to their glandular nature, we are quite unable as yet to decide whether the gland in question is the same gland as described by Burtt, owing to the fact that the latter did not mention which larval instar he had chosen. Secondly, the histological and the

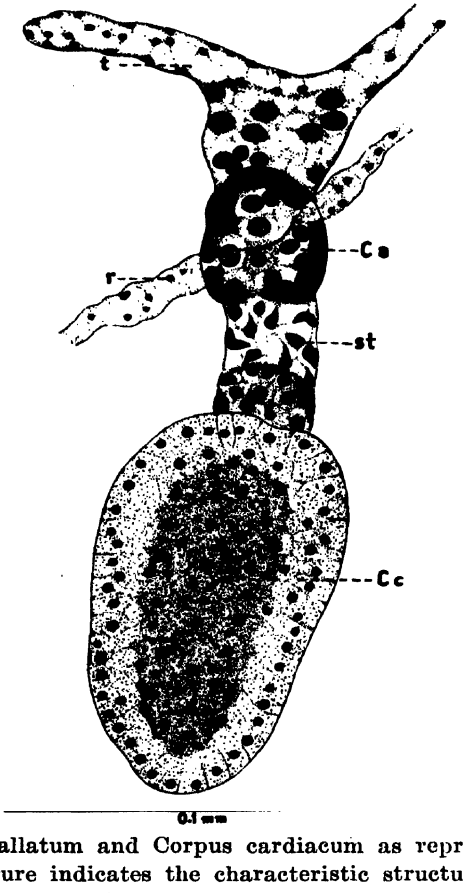
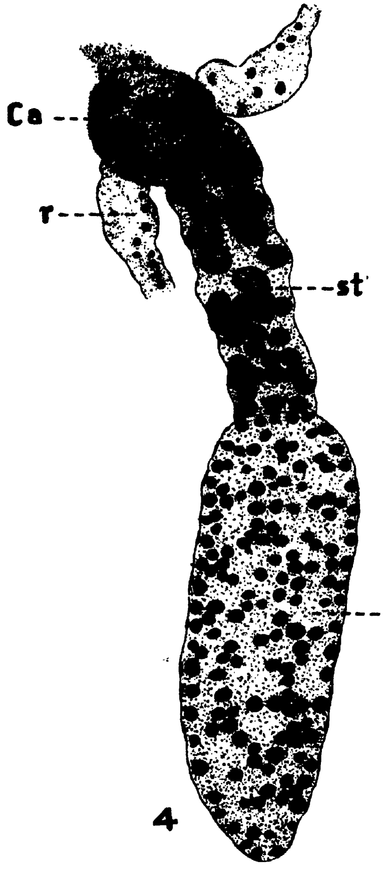


FIG. 3. Corpus allatum and Corpus cardiacum as represented in Fig. 2 magnified. The figure indicates the characteristic structures of the glands concerned in the last larval instar. C a, Corpus allatum; C c, Corpus cardiacum; r, recurrent nerve; s t, strand tissue; t, trachea.

anatomical features of the ellipsoid organs inform us that these bodies are really the Corpora cardiaca, which other authors sometimes call "oesophageal ganglia." As previously mentioned, the non-nervous structure of this endocrine gland has been made clear in the Orthoptera (De Lerma, 1937, and Pflugfelder, 1937).



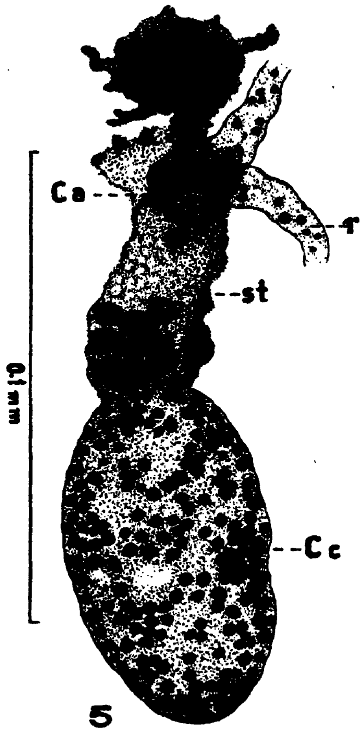
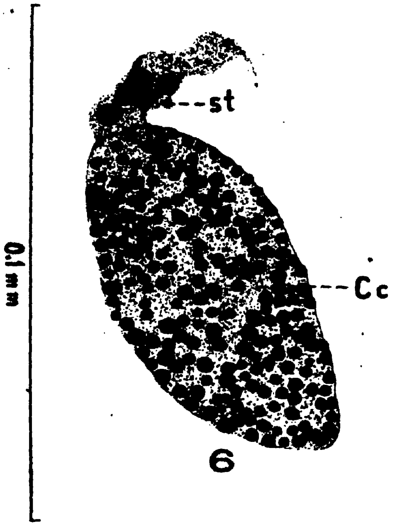


FIG. 4. Corpus allatum and Corpus cardiacum taken from a larva at the stage of thoracic swelling. The reduction in cell number and the size of Corpus allatum and the decrease in the distinctness of the cell boundaries and the size of Corpus cardiacum are all clearly shown. C a, Corpus allatum; C c, Corpus cardiacum; r, recurrent nerve; s t, strand tissue.

FIG. 5. Corpus allatum and Corpus cardiacum taken from a pupa at an early stage to show the degeneration of Corpus allatum and strand tissue, and the tendency of the nuclear pycnosis of the glandular cells of Corpus cardiacum. C a, corpus allatum; C c, Corpus cardiacum; r, recurrent nerve; s t, strand tissue.

For the present material, we are also unable to detect any nervous structure in these ellipsoid organs. So it seems more correct to call them Corpora cardiaca, instead of oesophageal ganglia. They are each composed of a great number of glandular cells. The observed changes of these two endocrine glands will now be given.

During the larval period, the increase in the body length of the larvae is accompanied by a corresponding increase in the size of Corpora allata. The glands, after having reached a mature condition, stop their growth in the last larval stage (Fig. 3).



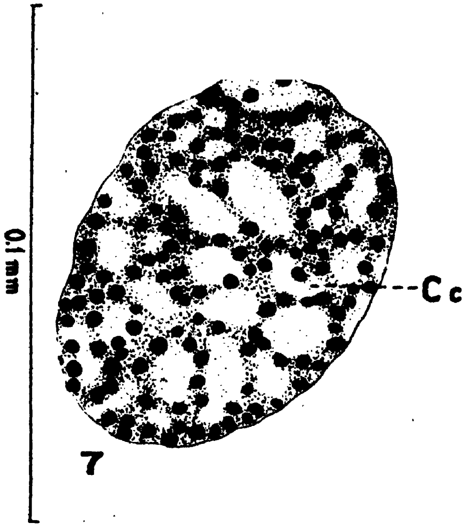


FIG. 6. Corpus cardiacum taken from a pupa at a later stage in which the Corpus allatum shows a complete atrophy and the strand tissue becomes very rudimentary. The nuclei of the glandular cells of Corpus cardiacum attained a highly pycnotic condition. C c, Corpus cardiacum; s t, strand tissue.

FIG. 7. Corpus cardiacum taken from an adult indicating a slight increase in the size of the gland. The strand tissue is no longer traceable at this stage. C c, Corpus cardiacum.

From this stage on, the larvae are now prepared to undergo pupation, as indicated by the characteristic enlargement of thoracic region (the stage of thoracic swelling). Then, the Corpus allatum begins to degenerate (Fig. 4). The degeneration process, characterized by the decrease in the distinctness of cell boundaries and the reduction of cell number (Figs. 4 and 5), leads to a complete atrophy of the gland later on (Fig. 6). In adults, the gland and its surrounding strand tissue are no longer traceable, as shown in Fig. 7.

Similarly, the Corpora cardiaca reach their maximum size in the last larval instar (Fig. 3). Their size then decreases gradually from the stage of thoracic swelling to the completion of pupation (Figs. 4–6), except, not infrequently, a slight increase in the adults (Fig. 7). The histological changes accompanying these form changes are: (1) The boundaries of individual glandular cells, which are clearly visible in the last larval instar, become indistinguishable at the onset of pupation; and (2) there is an increasing tendency for the condensation of nuclear materials from the stages of thoracic swelling onwards, so that in the pupa the gland is entirely provided with highly pycnotic nuclei. All these changes are clearly depicted in the figures.

Here then is the histological analysis of the Corpus allatum and Corpus cardiacum. The significant rôles played by them in the development of this insect, however, are not yet fully understood, owing to insufficient data. These will remain as problems for future investigation. From the existing evidence, it may safely be concluded that, at least for the material investigated, the Corpus allatum is a gland of holocrine type, while the Corpus cardiacum is definitely a merocrine gland.

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PARTIAL HERMAPHRODITISM AND DIGITAL ANOMALIES IN *NECTURUS MACULOSUS*

While conducting a laboratory in comparative anatomy certain abnormal individuals of *Necturus maculosus* were encountered that, in the opinion of the writer, were unusual enough to warrant special note and are here described.

The specimens concerned were purchased from the Biological Supply Company, Rochester, N. Y. Correspondence with that company revealed that these necturi were collected in Lake Winnebago, Wis., during the week preceding March 25, 1941.

In the collection were two males that were definitely abnormal. One specimen had a normal right testis with a greatly reduced left testis. By comparing a group of normal individuals it was determined that normal testes averaged 38.7 mm in length and 9.5 mm in width. In this first male, individual A, the reduced testis measured 13.0 mm in length and 2.5 mm in width. In all other respects this individual was normal.

The second male mentioned, individual B, had a normal right testis with dimensions of 35.5 mm in length and 12.0 mm in width, but instead of a testis on the left side there was a very poorly developed ovary. Normal ovaries of this lot measured 73.0 mm in length and 14.3 mm in width. The ovary of this individual measured 36.0 mm in length by 4.2 mm in width.

Critical examinations of this individual indicated that the Wolffian ducts on the two sides were not the same. The normal, right duct was of normal width and convoluted development, the average width of the duct was 1.5 mm. The Wolffian duct on the left side was not normally convoluted and was not as wide, 1.0 mm. The uriniferous tubules on the right side averaged 3 mm in length, while those on the left side were only 1.5 mm.

By removing the normal testis and comparing it histologically with a testis from a normal male it was found to be structurally normal. The gland on the left side, the vestigial ovary, clearly contained undeveloped ova. There was, however, no indication of a normal, female, functional Mullerian duct on the left side, thus preventing functional hermaphroditism.

The left fore foot of the same individual, individual B, possessed an extra phalanx extending from the side of digit number 3. By using the Alizarin red-staining and KOH-glycerine clearing technique the extra phalanx was clearly seen.

The right rear foot was very abnormal. Externally the foot appeared to have eight digits or two sets, one set superimposed over the other. By the Alizarin red, glycerine technique the double nature of the foot was clearly seen. There were six completely separate digits, metatarsals and phalanges. The fifth digits were fused at the base of the metatarsals. In addition to the abnormal digits it was seen that tarsal 2 was double with a separation of cartilages 4 and 5 into separate units.

Another specimen, individual C, possessed only three digits on the right fore foot. The Alizarin, glycerine technique indicated that digits 2 and 3 were fused at the distal ends of the corresponding metacarpals. The resulting digit contained only two phalanges, the normal number for digit 3.

The right rear foot of another specimen, individual D, possessed only three digits. By the Alizarin, glycerine technique it was determined that digit 4 was entirely absent. Either this digit had been lost or the fusion of digits 3 and 4 had been complete. Digit 5 on this same appendage contained only one phalanx instead of the normal two phalanges.

DISCUSSION

In considering the variations in the digits described here it may be said that they are possibly due simply to irregularities in embryonic development. However, in view of the observations of Blaufuss (1941) on the venous variations in necturus collected from this same region, Oshkosh and Winnebago, Wis., these anomalies may be the result of environmental causes. Jenness (1942) reported variations in digit number in necturus, but made no mention of the locality from which the animals were collected.

Much has been written on hermaphroditism in the Anura, but so far as the writer is able to determine no description has been made of natural hermaphrodites in the Caudata. As Bayliff (1940) indicated in his discussion of an hermaphrodite in *Rana catesbiana,* it is the interpretation of many that such individuals represent cases of sexual reversal, probably from female to male phase.

The condition in which the Wolffian ducts were found in the hermaphrodite here described was what would be expected in view of the observations of Humphrey (1941) and Rodgers and Risley (1938). Rodgers and Risley noted that the accessory urogenital ducts were influenced, quite early in development, by the associated gonad. Humphrey artificially produced hermaphrodites in *Ambystoma* and observed that the effects of the implanted gonads on the secondary sexual characters depended upon the sex type of the gonad under whose influence their differentiation first occurred.

In the necturus described here the right mesonephric duct and accessory structures were definitely under the influence of the normal testis found in connection with them. This duct on the left side was of the female type, logically under the influence of the ovary found there. However, the Mullerian duct on the left side was definitely of the male type, indicating the influence of the dominating testis. Also, the cloacal glands were of the male type, much swollen and highly glandular.

These observations seem to indicate that this animal did not represent an individual undergoing a sexual phase shift. Certainly if there was a phase shift in process here it was not from female to male which seems to be the usual type of shift reported for the Anura. The writer assumes that this individual presents an irregularity in development and not a shift in phases.

The probability is suggested that this individual represented one in which the bisexual state in development was persistent. Later in development the testis quite definitely assumed a permanent, dominating nature. As suggested above, such an irregularity may be the result of environmental factors of an undetermined nature.

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THE
AMERICAN NATURALIST

VOL. LXXVIII November–December, 1944 No. 779

RESPONSES OF CAPTIVE ALLIGATORS TO AUDITORY STIMULATION[1]

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INTRODUCTION

THREE types of vocalization have been described for the American alligator (*Alligator mississipiensis*) and speculations have been offered as to the significance of each call. A series of short grunts, "umph! umph! umph!" may be given by the animals from birth to maturity according to McIlhenny (1935) who recorded the emission of this sound by a male which was attacked by another of its species. A sharp "hiss" occurs frequently when the alligator is "disturbed" (Berridge, 1926) or "angry" (McIlhenny, 1935); and the hiss may be combined with the roar when one adult male is "seeking encounter" with another (McIlhenny, 1935).

The bellowing or roaring of the full-grown alligator has been described by many observers. In the Southeastern United States this reptile breeds during early summer, and it is at this time that roaring is most frequently heard (True, 1893; Reese, 1907; Harper, 1930; McIlhenny, 1935). Roaring continues with diminishing frequency throughout the warm summer months and is rare during the winter (Harper, 1930; McIlhenny, 1935). We have been unable to find any published accounts of observed matings in *Alligator mississipiensis,* but according to Descourtilz (1809) a closely related species ("Caiman") roars during copulation; and Wosseler (1915), who observed the courtship of Nile crocodiles (*Crocodylus niloticus*) in the Hamburg Zoological Gardens, reports that similar vocalization occurs in this species.

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[1] Contribution from the Department of Animal Behavior, The American Museum of Natural History, New York, N. Y.

Although the point is not conclusively established it is probable that the roar is emitted only by the male alligator. Similarly, in the crocodile (*C. niloticus*) it is apparently only the male that roars (Schmidt, 1919). The function of the call has been variously interpreted. Harper (1930) suggests that it may serve as a mating call during breeding season, but this is obviously not an exclusive function, since the roar also occurs at other times of the year. McIlhenny (1935) believes that the male's roar is a challenge to other breeding males and holds no attraction for the female of the species. In the course of field observations both Harper and McIlhenny found that the roaring of one male is very likely to stimulate similar vocalization on the part of others in the vicinity; in fact, McIlhenny states that if other adult males are within hearing they are certain to answer.

The roar has been described by different authors as a "loud, deep-toned booming sound" (Berridge, 1926), and as "something like [the cry of] a bull frog, but intensified like distant thunder" (True, 1893). According to McIlhenny (1935) there is "no sound natural or artificial which causes such a tremendous vibration of the atmosphere." Ditmars (1910) states that although 5-foot males can roar, the sound produced by a 10- to 12-foot specimen is very much louder. The roar of an adult bull is said to be audible for at least three miles. The Caiman's "angry roar" (Descourtilz, 1809) and the Nile crocodile's "gasping roar" (Wosseler, 1915) are apparently quite similar to the vocalization of the American alligator.

The position and behavior of the alligator at the time of roaring has been observed by Harper (1930) and by McIlhenny (1935) whose accounts agree in all essential details. Roaring occurs most frequently when the alligator is swimming or floating in the water. Occasionally an animal may roar when it is half in the water and half on the bank; but McIlhenny states that this call is never given when the reptile's body is entirely on land. When the alligator roars while in the water the head is thrown upward at a sharp angle to the back and points out of the water at an angle of 30 to 40 degrees. The tail is raised in an arc above the water and the tip bends downward to touch the surface. The tail is moved from side to side and the alligator thus "sculls" himself along between roars. Just before each roar there is a deep inhalation; the body is inflated and the throat puffed out. During the subsequent exhalation the entire body cavity is contracted in a series of powerful, spasmodic jerks. It is during the exhalation that the head and tail are raised highest out of the water. Each roar lasts for approximately one second according to Harper and 3.5 to 7 seconds according to McIlhenny. After the roar the head and tail are lowered, and the central portions of the body rise. In Harper's experience the next roar follows after an interval of two to three seconds, and there are very few repetitions. McIlhenny estimated the interval between roars to be about two minutes and reported that in some instances 12 or more roars were emitted in succession. The alternate sinking and rising of the body is probably related to changes in specific gravity accompanying inflation and deflation of the lungs (Harper, 1930).

When the head is raised out of the water, musk glands situated in the skin of the lower jaw are opened (Ditmars, 1910); and McIlhenny (1935) describes the "sweet pungent musk [which] scents the air and water and lingers for several hours."

ROARING IN A CAPTIVE ALLIGATOR

Four male alligators (*mississipiensis*) were maintained for several years in the laboratories of the Department of Animal Behavior at the American Museum of Natural

History. These animals had been given to the museum by tourists who purchased them during trips to Florida. In view of the fact that such specimens are usually sold while they are quite small it is probable that none of our alligators had had any extensive contact with wild adults of their own species. The reptiles ranged in length from 2 feet 4 inches to 5 feet 1 inch. Since alligators are about 8 to 10 inches long at hatching, and grow approximately 12 inches a year (McIlhenny, 1935), it is likely that the oldest of our animals was somewhat over five years of age. During the early stages of their captivity at the museum all four alligators were kept in the same tank and fed fish and beef heart three times a week.

The three smaller reptiles not infrequently emitted a call consisting of a series of short grunts, which might be written "umph! umph! umph!," and seemed to be elicited by contact with other alligators. So far as we could see the animals made no response when this sound was given by one of their number. The largest alligator could easily be induced to give a loud, prolonged "hiss," and this sound was evoked by noxious stimuli of various sorts such as poking the animal with a stick, turning a blast of air in his face or pouring water into the tank near his head. When the "hiss" occurs the alligator's mouth is held partly open, exposing the teeth. Although some of the smaller alligators were stimulated to "hiss" upon a few occasions the reaction was most easily and frequently evoked in the largest reptile.

After the alligators had been in the laboratory, approximately two years it was accidentally discovered that the largest animal (but none of the others) could be stimulated to roar in response to a particular sound. Following this discovery various tests were conducted one day each week for 18 weeks (January 8 to May 21) to obtain data for a detailed description of the reptile's response to tones of different frequency and quality.[2] The results are less complete than we would wish, for it became necessary to discontinue the testing temporarily, and before observations could be resumed the alligator died. Since there is no immediate opportunity for extending the investigations we are reporting our incomplete data in the hope that they will prove of use to others who may be in a position to verify and extend them.

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[2] Miss Eleanor Herrick's assistance in the conduction of these tests is gratefully acknowledged.

Original Effective Stimulus. In the museum laboratory are several glass-sided aquaria, the soapstone ends of which are connected on the outside of the glass by steel rods ¼ inch in diameter and 3 feet in length. Both ends of each rod are threaded, and nuts fastened on the outside of the stone ends are tightened to hold the stone firmly against the ends of the glass sides. Accordingly, the slender rods are always under considerable tension; and when one is plucked like the string of a musical instrument it vibrates for several seconds, producing a deep-toned, thrumming sound. It was in response to this sound that we first accidentally elicited roaring in the largest of the four alligators.[3]

Following our discovery of the reptile's responsiveness to this type of auditory stimulation he was transferred to a separate tank 17 feet long, 29 inches wide and 23 inches deep. Approximately 8 inches of water was kept in the tank and the room temperature was held at 80° ± 1 F. Under these conditions the alligator's reactions to vibrations of the steel rod were tested one day each week for 11 successive weeks. Roaring occurred several times on each test day, although it was not evoked every time that the rod was activated.

Preliminary tests revealed that roaring was elicited when the rod was plucked once every 5 to 10 seconds and allowed to vibrate freely during the intervals. Activating the rod repeatedly at shorter intervals produced a steady volume of sound which failed to evoke the response; and plucking the rod once a minute or less frequently was equally ineffective. In all subsequent tests the rod was plucked at 5 to 10 second intervals until the first roar sounded or until it was judged that no response was going to occur. The initial roar was usually given after the rod had been activated 2 to 8 times; but under special conditions as many as 72 applications of the stimulus were necessary to call out the response, and in occasional tests no vocalization occurred.

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[3] In preparing this report we have assumed that the effective stimulus was exclusively auditory. There is of course some possibility (which we consider remote) that the animal responded to tactile stimulation arising from vibrations of the substratum. It seems to us that conditions of the various tests render such an interpretation unlikely; but the absence of a strict control of the vibratory factor should be noted.

Bodily Changes Accompanying Roaring. Analysis of motion pictures which were taken while the alligator roared provides the basis for a detailed description of the postural changes occurring during production of the roar. At the beginning of the first roar the alligator's head is raised above the water, and as inhalation occurs the sides swell noticeably and the central portions of the body, becoming more buoyant, rise. The subsequent exhalation, which is responsible for the production of sound, starts with a general compression of the lateral body walls in which muscular contraction appears to be fairly evenly distributed along the sides between the front and rear legs. This brief, initial contraction is followed immediately by spasmodic compression of the anterior portion of the sides just behind the forelimbs, with concomitant inflation of the more posterior sections of the lateral body wall. It is as though the extreme contraction in the thoracic area resulted in displacement of internal organs, temporarily forcing them posteriorly to distend the lateral abdominal wall.

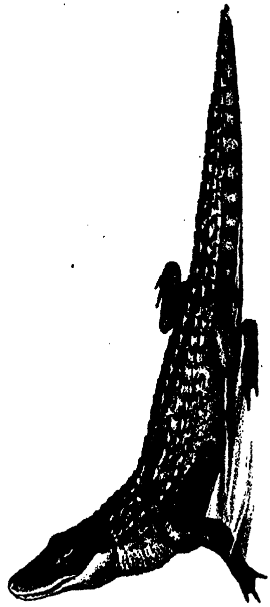
The force of the second contraction is often sufficient to drive the animal backward in the water. This second and more powerful phase of the bodily contraction is accompanied by a sharp increase in the elevation of the head and a marked downward movement of the central portions of the body. Several roars usually occur in sequence, and with each succeeding vocalization the head is raised higher, so that after several roars it is at a sharp angle with the line of the back. During roaring there is a pronounced tendency to raise the anterior parts of the body by extending the front legs; and in connection with the most extreme roars the tail is raised slightly above the surface of the water. At the conclusion of the last roar the alligator may relax at once, lowering the head to the water level; but in the majority of instances the extreme elevation of the head and extension of the forelimbs is maintained in a motionless pose for several minutes. In 21 tests the pose was held for an average of 5 minutes after the final roar, and in a few cases the interval between the cessation of vocalization and general relaxation was longer (maximum 16 minutes). The various postural changes associated with roaring are illustrated in Fig. 1.

The postural changes described above accompanied roaring in almost every instance, but they are not inevitable and essential concomitants of the vocal response, for upon rare occasions roars were delivered when the alligator was lying nearly flat in the water or standing with the legs fully extended so that the body was raised as high as possible and held parallel to the water.

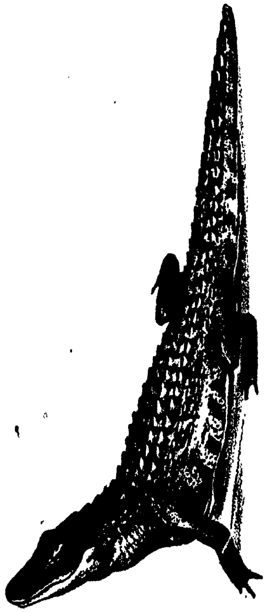
Our observations were made while the alligator was in approximately 8 inches of water which failed to cover his back; whereas the descriptions of roaring recorded by Harper (1930) and McIlhenny (1935) were based upon the behavior of swimming animals. Considering the differences in conditions under which observation occurred our account agrees closely with those of the earlier workers, and we are convinced that had our animal been tested in deeper water the pattern would have been identical with the behavior observed in the wild.

At no time was there any indication that our animal released the musk which is said to be emitted by wild alligators when they roar.

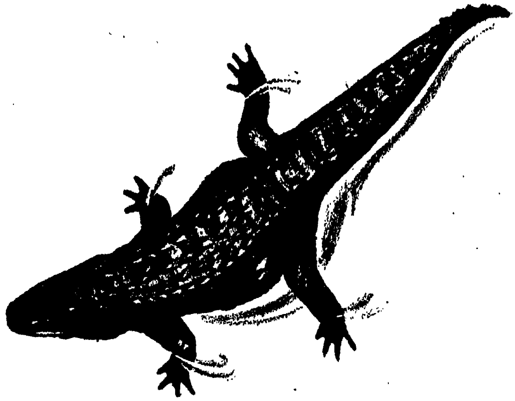
Occasionally when the alligator inhales preparatory to roaring there occurs a short "hic" sound just at the end



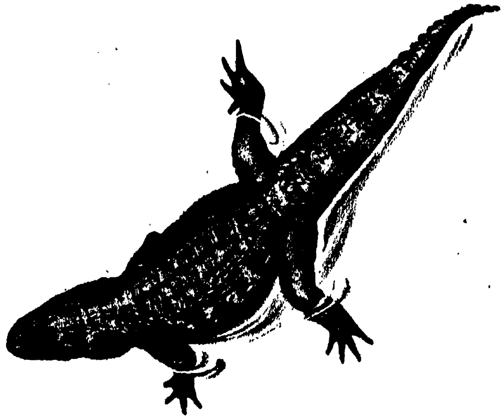
FINAL EXHALATION—LATERAL VIEW



PRELIMINARY INHALATION—LATERAL VIEW



FINAL EXHALATION—DORSAL VIEW



PRELIMINARY INHALATION—DORSAL VIEW

of the inhalation. Each of the two phases of the muscular contraction accompanying exhalation produces a distinct sound. The initial, general compression of the sides produces a moderately loud, deep note; and as the subsequent extreme lateral contraction of the anterior body cavity occurs the volume of this beginning note is suddenly, tremendously increased in very sharp crescendo, and at the same time the pitch rises appreciably. After coming suddenly to its peak the volume of sound dies out slowly and the pitch falls concomitantly. The entire roar lasts approximately one second and the beginning note takes up only the first one-fifth of this period. (Harper estimated the duration of the roar to be one second.) The alligator's mouth is opened less than ½ inch if at all during inhalation and subsequent emission of the roar.

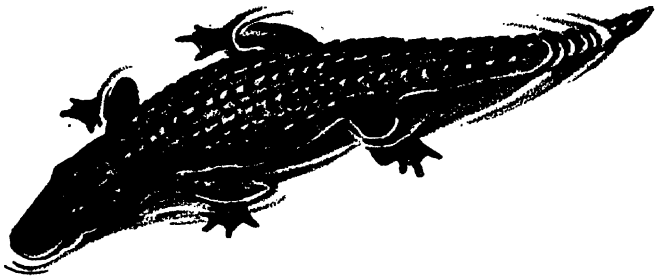
Frequency of Roaring. The alligator's reactions to the vibrating steel rod were observed one day each week for 11 weeks; and several tests were given each day. The rod was plucked at 5-second intervals until the first roar was elicited, and usually several successive roars then occurred without further stimulation. In 30 tests the number of consecutive roars varied from one to ten with an average of 7.4, but each of the extreme values occurred only once; and in 24 of the 30 instances the range was 6–8. When several roars were uttered in succession the intra-roar interval, as measured in 22 tests, ranged from 4.5 to 6.5 seconds. (Harper's estimation of the interval was 2 to 3 seconds.) In three instances longer intervals were recorded but these were unusual.

Occasionally the auditory stimulus was applied without eliciting any vocal response; but this usually occurred when a positive reaction had been obtained a short time before. To test the possibility that a series of roars is followed by a refractory period during which responsiveness to the auditory stimulus is reduced we attempted to exhaust the response by repeated stimulations. The rod was plucked until roaring began, and as soon as the alligator ceased roaring and relaxed, stimulation was resumed. This process was repeated 5 times. The number of rod-activations necessary to evoke roaring in each successive instance was as follows: 26, 7, 47, 72, 51. We have here a rough indication that the response may become more difficult to obtain in successive tests which are very closely spaced. It is interesting to note, however, that the number of roars elicited by successive stimulations shows no tendency to diminish. The total number of roars sounded in each of these 5 tests was: 8, 6, 6, 7, 8. The number of roars that occur in a given response is apparently independent of the number of times the stimulus is applied before roaring begins. These findings suggest that roaring may be somewhat of an all-or-none reaction, and that a threshold phenomenon is involved.

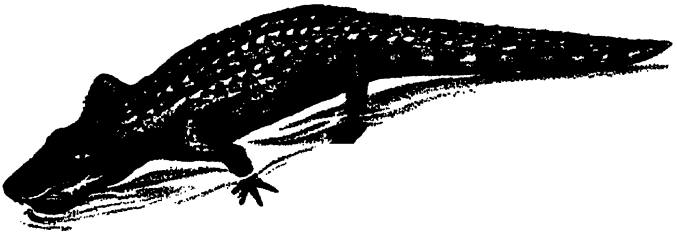
Behavioral Changes Accompanying Roaring. Upon several occasions the alligator was tested in dim light. Before auditory stimulation began the vertical, slit-like pupil of the eye was always partially contracted, but after roaring it was invariably maximally expanded into a broad oval. Involvement of the autonomic nervous system is indicated. There were many other indications that the alligator was highly excited by the auditory stimulus. Under ordinary conditions he was extremely lethargic and unresponsive to environmental stimuli. Frequently when the rod was vibrated the alligator rushed to a point in the tank closest to the stimulus and slashed his tail back and forth several times before roaring. In many tests the animal repeatedly tried to force himself up and over the side of the tank, and these attempts were always made at the point nearest the position of the vibrating rod. When stimulation was resumed immediately after roaring ceased the reptile's apparent agitation increased, and he moved rapidly back and forth shoving against the wall of the tank nearest the stimulus and thrashing his tail rapidly from side to side.

In some tests the manner in which the alligator moved toward the source of sound involved the adoption of a distinctive posture and method of locomotion which for conveninence we have termed the "aggressive approach." In this behavior pattern the body is raised as high as full extension of all four limbs will permit; and as the animal walks the stepping reactions are slow and deliberate. The head and tail are held low, and elevation of the central portions of the body produces a distinct, convex arching of the back. The lateral body walls are distended to the fullest extent, appreciably increasing the animal's girth; and frequently when this posture is assumed the mouth is held half open. The postures of the alligator during the "aggressive approach" and during the more common type of locomotion, in which the body is low in the water, are shown in Fig. 2.

TWO TYPES OF LOCOMOTION IN ALLIGATOR MISSISSIPIENSIS



USUAL WALKING POSTURE



"AGGRESSIVE APPROACH" POSTURE

FIG. 2.

The "high walk" of the alligator has been compared by Schaeffer (1941) to the type of locomotion which was probably exhibited by advanced therapsids such as *Bauria.* Both Schaeffer and Huene (1913) refer to the "high walk" in alligators and crocodiles as a method of rapid locomotion in contrast to the slower rate of progression achieved by walking with the limbs spread out and ventral surfaces dragging on the ground. Our observations indicate that when it is employed in the "aggressive approach" the "high walk" of the alligator is performed, not rapidly, but with very slow and deliberate movements.

Localization of the Source of Sound. In addition to roaring when the steel rod was vibrated the alligator made various responses which revealed his ability not only to hear but to localize the sound. In the majority of tests when the vibrating rod was employed the alligator moved to a position in the tank as close as possible to the source of the sound. Upon many occasions this reaction involved moving the full length of the tank (17 feet). Usually the approach was made before roaring occurred; but occasionally the roar was given and then the animal relaxed and moved swiftly to the source of stimulation. In one instance when the stimulus was presented the full length of the tank away from the alligator he roared without changing position and then, as the stimulation was resumed, moved quickly down to the other end and roared again.

In another test the rod was vibrated constantly while it was moved (on a small truck) from one end of the tank to the other and back again several times. The apparatus and the experimenter were well below the top of the sides of the alligator's tank, and thus completely beyond his visual field. As the vibrating rod passed back and forth on the outside of the tank the animal moved parallel with it on the inside. No roaring occurred, but the alligator followed the invisible stimulus closely without interruption for 10 minutes, and throughout this period he made repeated and vigorous attempts to raise his body to the top of the tank wall.

In tests to be described below several types of auditory stimuli were employed which did not elicit roaring, but in many instances the alligator's reactions conclusively demonstrated his ability to localize these sounds. Sometimes the animal moved part way to the source of stimulation, and in other tests the head was raised and turned toward the sound.

Although it seemed obvious that the alligator's vocal response and localizing reactions depended exclusively upon auditory stimulation a special test was conducted to rule out all possible visual cues. The animal's tank was completely covered with heavy black tar paper; yet under these conditions when the steel rod was vibrated roaring occurred promptly. The test was repeated several times with positive results, and when the tank covering was removed immediately after the final roar it was found that the alligator had moved as close as possible to the source of sound.

Since McIlhenny (1935) stated that he had never observed alligators roaring unless they were at least partly in the water, we conducted two tests to determine whether the response could be evoked with the animal in a dry tank. The tank was drained and the stimulus of the vibrating rod applied. The reptile roared readily in both tests and his behavior did not appear to be affected by the absence of water. In one test he showed the "aggressive approach" and came directly to the source of stimulation.

Response to Other Types of Auditory Stimuli. In all the observations described above a single type of auditory stimulation was employed, namely, the sound produced by the vibrating rod. Additional tests were conducted to determine the alligator's reactions to other sounds. The results of the supplementary experiments indicated that roaring could be evoked only by auditory stimuli of rather specific frequencies, namely, frequencies near that of the animal's own roar, or the first harmonic thereof.

Loud noises of various types were used in several tests without eliciting any observable response. Repeated stimulations with a large electric buzzer or an electric bell sounded separately and simultaneously elicited no behavioral reactions.[4] Tuning forks with frequencies varying from 256 ∼ to 4098 ∼ were used as stimuli on two test days.[5] The forks were vibrated singly and in various combinations but in no instance did the alligator give any observable response.

By comparing the sound of the vibrating rod with the various notes on the diatonic scale we determined that, although many partials or harmonics were audible, the fundamental note was approximately equal to B flat two octaves below middle C. This note, which seemed to have roughly the same pitch as the alligator's roar, is produced by 57 vibrations per second.[6] Unfortunately no apparatus was available which would produce pure tones of low frequency and high volume. As a substitute measure we investigated the possibility of using as a source of stimulation tones produced by various musical instruments; and after some exploration it was found that a sound closely resembling that emitted by the rod could be produced on the French horn. Accordingly, the reactions of the alligator to the tones of this instrument were tested.

The animal was stimulated to roar when a note produced by 57 ∼ (B♭ 2 octaves below middle C) was blown at 5-second intervals with a 2-second rest after each note. If the same tone was sounded continuously no roaring occurred. This tone, sounded at intervals, was used as a stimulus in 10 tests and roaring was produced in every instance. The animal's reactions to the 57 ∼ tone of the French horn were the same as those given to the vibrating steel rod. Postural changes, evidence of excitement and accurate localizing behavior were identical for the two types of stimuli.

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[4] There have come to our attention anecdotal accounts of alligators roaring after a shotgun had been fired close by. None of our stimuli was as loud as a gunshot, and there is a possibility that greater volume would have proven effective in eliciting the roar.

[5] The exact frequencies tested were as follows: 256, 320, 512, 640, 768, 896 1,024, 1,152, 2,048 and 4,098.

[6] All the frequencies mentioned in this report are approximate, but the maximum error is not more than 2 vibrations per second in either direction.

Other tones with frequencies close to 57 ~ failed to evoke roaring, but the reaction was elicited with some difficulty in response to the first harmonic of 57 ~, namely 113 ~ (B♭ 1 octave below middle C). This note was used in 5 tests and roaring occurred in only one, indicating that the higher frequency (first harmonic) was less effective than the lower (fundamental). In 2 tests although the reptile did not roar in response to 113 ~ he did move toward the source of sound. No other tone or combination of tones produced by the French horn stimulated roaring, but several frequencies elicited behavioral responses indicating that they were within the animal's auditory range. A list of the frequencies tested with notes on behavior is presented in Table I.

TABLE 1

RESPONSES OF AN AMERICAN ALLIGATOR TO VARIOUS TONES PRODUCED BY THE FRENCH HORN

Auditory stimulus		Behavior of alligator
Note on diatonic scale	Vibrations per second	
B♭ 2 octaves below middle C	57	Roared in every test
A and B♭ trill 1 octave below middle C	107 + 113	Opened mouth widely
B♭ 1 octave below middle C	113	Roared in 1 test; localized source of sound in all other tests
A and B♭ trill immediately below middle C	213 + 227	Hissed
B♭ immediately below middle C	227	Raised head; came to source of sound; hissed
E and F trill above middle C	320 + 341	Moved head toward sound; hissed
A and B♭ trill 1 octave above middle C	426 + 453	None

The various tones were not tested extensively, but there appears to be sufficient evidence to indicate that the alligator was sensitive to a greater or less degree to frequencies between 57 ~ and 341 ~; and that roaring occurred most readily in response to 57 ~, although it could occasionally be elicited by the first harmonic of that frequency. It should be noted that tuning forks with frequencies of 256 ~ and 320 ~ elicited no response on the part of the alligator, whereas tones of the French horn within this range, although this did not induce roaring, did prove audible to the animal. It seems likely that differences in volume or in the quality of the stimulus were responsible for this difference in responsiveness.

To determine the possible effects of varying the quality of the stimulus while holding the frequency constant we tested the response of the alligator to various notes played on a 'cello. The frequencies which had proven effective in the case of the French horn were found capable of evoking roaring when the stringed instrument was employed as the source of sound. A note of 57 ~ played at 5 second intervals always stimulated the animal to roar (3 tests), and a tone one octave higher (113 ~) induced this reaction occasionally. Other notes or combination of notes failed to call forth any vocal response.

Response to Phonographic Recordings. Phonographic recordings were made of the alligator's roar and of the sound of the vibrating steel rod and the French horn (blown at 57 ~). The fidelity of reproduction was not high, but recordings of the French horn and of the alligator's own roar called forth answering roars in several tests; and in every instance the animal appeared to be highly excited, moving rapidly up and down the tank with his tail slashing in a wide arc, and frequently assuming the "aggressive approach" posture. When the record of the rod's vibration was played on a small portable phonograph the animal hissed several times, but failed to roar.

BEHAVIOR TOWARD OTHER ALLIGATORS

It is generally agreed (True, 1893; Reese, 1907; Harper, 1930; McIlhenny, 1935) that alligators roar most frequently during breeding season, and it is at this time particularly that males are strongly aggressive and fight among themselves a great deal. Since roaring seems to be associated with certain types of social behavior, and since our animal gave evidence of being highly excited when he was stimulated to roar, it was of interest to investigate his reactions to another alligator during tests in which the effective auditory stimulus was applied. Accordingly, during 4 different test days we placed the second largest animal (length, 4 feet 10 inches) in the tank with the male who roared. On the first 2 test days each time the large alligator roared the smaller animal approached him uttering the "umph!" sound described earlier. The larger reptile seemed to pay no attention to the smaller, and often crawled over him while moving toward the source of auditory stimulation. Upon such occasions the smaller alligator gave no evidence of being excited, but emitted the "umph!" call when touched.

On the third test day the large alligator was stimulated to roar and immediately thereafter the smaller individual was introduced into the tank. The larger animal at once assumed the "aggressive approach" posture and moved toward the smaller male. The large reptile halted about 18 inches away from the other alligator maintaining the aggressive pose, and the smaller individual, who had retreated into one corner of the tank, slashed his tail rapidly from side to side whereupon the large alligator backed away and relaxed. Several times thereafter the large male advanced upon the smaller employing the "aggressive approach." In each instance the smaller male fled to the farthest end of the tank, but the aggressor pressed his advantage only so far, always halting before actual contact was established.

Approximately one month later the smaller alligator was returned to the larger animal's tank for a fourth test and the latter immediately showed the "aggressive approach." In this case, as in the preceding test, the smaller reptile appeared to be highly excited by the "aggressive approach" of the other male and moved quickly to the far end of the tank. The larger alligator pursued, cornered the other animal in one end of the narrow tank, made a final lunge and bit him severely. The smaller individual slipped past the attacking male, but was pursued and bitten again. This type of interaction between the two alligators was repeated several times with the larger animal always assuming the aggressive rôle and the smaller individual seeking only to escape. The large male's attack was not restricted to any particular part of the smaller alligator's body; but head, limbs and tail were seized and bitten indiscriminately.

The largest male's tendency to attack a second alligator was quite probably related to general excitement resulting from auditory stimulation presented earlier on the same days; and in addition tonal stimuli delivered while the second animal was in the tank appeared to increase the frequency of the "aggressive approach." However a close temporal relationship between roaring and attack was not apparent. It is possible that some sort of "territory defense" was also involved. For more than a year prior to the experiments herein reported all four alligators had been kept together in one tank and no fighting occurred at any time. Then for several months the largest individual lived alone in a much larger space. It is not unlikely that his attacks upon the second male suddenly introduced into his solitary tank were in the nature of territory defense intensified somewhat by auditory stimulation. Harper (1930) has pointed out that adult alligators in the wild often live in small "'gator holes" and suggests that they "probably exercise some sort of proprietory rights over [their] home territory."

To determine whether any territorial behavior could be elicited the four alligators were released in an outdoor pen 24 feet square. One corner of the area was flooded to form a pool some 15 feet across and 6 to 12 inches deep. Although they lived in the large pen for more than a month none of the animals showed any tendency to establish individual territories. On the contrary, they usually stayed close together, sometimes in the water and sometimes in the dry portions of the pen. When the observer approached, all four animals moved away and all but the smallest hissed. Upon 2 days while the alligators were outdoors the steel rod was vibrated in an attempt to induce roaring. At the first test the largest alligator approached the sound, then went into the water and roared. Upon other occasions he made no response unless the stimulus was within a few feet, in which case roaring occurred. Under these conditions no aggressive reactions toward other alligators were observed.

ROARING IN A SECOND ALLIGATOR

Only one of the four alligators in the Museum laboratory could be induced to roar in response to an auditory stimulus. Since the other three individuals were smaller and undoubtedly younger we wished to repeat our tests using another large alligator. A single series of observations was conducted at the New York Aquarium through the courtesy of its director, Dr. C. M. Breder. In the large indoor pool were five *Alligator mississipiensis,* one Chinese alligator (*A. sinensis*) and one American crocodile (*C. acutus*). Recordings of the roar emitted by the alligator at the Museum and of the sound produced by the vigrating steel rod were played at the Aquarium, but the sound was very weak in a large room and the only response elicited was some head movement on the part of two *A. mississipiensis.*

The French horn was blown at 5-second intervals (frequency 57 ∼) for several minutes, and the largest *Alligator mississipiensis* roared twice in reply. The test was repeated 3 times and 4 roars occurred in each test. None of the other animals gave any vocal reactions, but several of them swam toward the sound.

The alligator which roared in response to the French horn was larger than the Museum animal (approximately 7 feet in length) and his roar was of lower pitch. After several roars had occurred the pupil of the eye was noticeably dilated. At the Aquarium the alligators swam in water several feet deep, and this resulted in somewhat different postural adjustments during roaring. The head was elevated at a sharp angle; the back was concavely arched; and the tail was raised out of the water with the tip bending downward to touch the surface. Each time the animal roared the strong contraction in the lateral thoracic region resulted in a marked downward movement of the body, and the following inhalation raised the body again; so that as a series of roars was emitted the alligator bobbed up and down in the water repeatedly. This description agrees closely with those of Harper (1930) and of McIlhenny (1935) who observed the behavior in wild alligators; although the emission of musk reported by these writers was not observed in the case of the Aquarium specimen.

DISCUSSION

Controlled laboratory experiments have shown that many amphibia respond to air-borne sounds (Yerkes, 1905; Bruyn and Van Nifterick, 1920; Patterson, 1920); and field observations indicate that auditory stimuli play an important rôle in the lives of some frogs and toads (Noble, 1931). There is a good deal of evidence to suggest that a true auditory sensitivity is lacking in most reptilian species. Kuroda (1923), working with the Japanese pond turtle (*Clemmys japonica*), was unable to obtain any reaction to sounds; and other turtles, tortoises and snakes are apparently equally unresponsive to auditory stimulation (Beatty, 1932; Evans, 1935b). Studies of electrical activity in the eighth nerve support the conclusions based upon observations of behavior. In the grass snake (*Natrix natrix*) loud sounds produce no activity in the eighth nerve; and in the common land tortoise and the box tortoise (*Terrapene*), although action currents occur when the ear is exposed to sound, the currents in the nerve are due entirely to action potentials in its fibers and the animals "give no sign of appreciating the sounds to which their ears are sensitive" (Adrian, 1938).

Several observers have noted that some lizards are sensitive to sounds. Kuroda (1923) found that *Tachydromus tachydromoidae* shows a modification of certain visual reflexes when stimulated with a bell or with a Galton whistle. According to Beatty (1932) the green lizard (*Lacerta viridis*) responds to auditory stimuli; and Berger found that *Lacerta agilis* and *L. vipipara* exhibited specific eye reflexes, modified their respiratory rhythm, and could be trained to execute learned responses to loud noises as well as tonal stimuli.

The alligators and crocodiles have a membranous ear drum, a true cochlea (Adrian, 1938) and a tectorial membrane (Evans, 1935b); and in the alligator a true Wever and Bray effect is obtainable. As in birds and mammals electrical oscillations corresponding in frequency to the sound stimulus can be picked up from any part of the inner ear, and cochlear potentials spread into the eighth nerve (Adrian, 1938). Thus the anatomic and physiological basis for hearing is present.

Evans (1935b) has pointed out some interesting correlations between the proportions of certain inner ear structures and the presence or absence of "vocality." He emphasizes the fact that among the amniotes good evidence for vocality is available only for gecko lizards, alligators, birds and mammals. Turtles, snakes and all lizards except geckos are non-vocal according to Evans (since hissing is not accepted as "true vocality"). When the length of the cochlea is compared to that of the lagena the ratio is found to be 0.5:1 in turtles (4 species), 0.5:1 in snakes (5 species), and 1.28:1 in all lizards except skinks and geckos (8 species). Relative cochlear length is increased in the skink so that the cochlea/lagena ratio is 2.64:1, and in this group vocality may exist, although this is not certain. In geckos (*Gymnodactylus kotschyi* and *Hemidactylus turcicus*) the ratio becomes 3.2:1; and these species are quite vocal, employing their calls especially during breeding season. The alligator has a cochlea/lagena length ratio of 4.7:1, and is known to vocalize extensively under certain conditions. Evans concludes that "the cochlea must bear a length ratio of 3:1 to the lagena before any amniote is capable of modifying its social behavior (particularly fighting and mating) by means of vocality."

Field observations strongly suggest that in the alligator vocal expression forms an integral part of certain behavior patterns, but there is a paucity of experimental evidence regarding either audition or vocalization in alligators or crocodiles. Reese (1923) tested the response of *A. mississipiensis* to thermal, visual, chemical and gravitational stimuli, but gives no evidence regarding effects of sound impulses. Berger (1924) found that the West African short-snouted crocodile (*Osteolaemus tetraspis*) altered its rate of breathing in response to the sound of an electric bell, a siren or the firing of a blank cartridge. Present results suggest that *A. mississipiensis* is capable of hearing sounds between 57 ~ and 341 ~, and since other frequencies were not explored the range of sensitivity may be much greater than these values would indicate. Furthermore, the animal's ability to localize accurately the source of auditory stimulation seems clearly established by our data.

Results of this investigation appear to have some bearing upon the interpretation of possible functions of the vocal response. Various observers have stated that when one adult bull alligator roars others will reply; and our laboratory tests (particularly those involving the response to a recording of the roar) give support to this conclusion. It will be recalled that the roar has been variously interpreted as a mating call by which the females are attracted to the male (Harper, 1930), and as a challenge to other adult males (McIlhenny, 1935). In this connection the behavioral responses of our specimen to 57 ~ stimulus are of particular interest. In nearly every instance the male moved as close as possible to the source of the sound; and in many tests the method of progression involved the display of the "aggressive approach."

The "aggressive approach" pattern in the alligator is strikingly similar to the postural responses shown by some lizards during fighting and/or preliminary courtship. The male eastern whip-tailed lizard (*Cnemidophorus sexlineatus*) when approached by another lizard rises high on his legs, automatically displaying his bright, blue ventral surfaces. A similar reaction is made by the eastern fence-lizard (*Sceloporus undulatus*); and this type of behavior has been interpreted as assisting in sex recognition, since it is usually shown only by the male (Noble and Bradley, 1933). In fighting, the western banded gecko (*Coleonyx variegatus* Baird) rises high on all four legs, arches his back and holds his head low (Greenberg, 1943). The male American chameleon (*Anolis carolinensis*) raises his body as high as possible prior to attacking other males (Evans, 1935a).

The manner in which the alligator that we observed approached the source of stimulation and the nature of his subsequent reactions to a second male lead us to suspect that the auditory stimulation and the resultant vocalization were associated with emotional excitement and an increased tendency toward actively aggressive behavior. It seems probable that under natural conditions the roars of the breeding male are likely to arouse aggressive responses in other males, and possibly to increase fighting since other alligators may seek out the vocal individual. It is of course also conceivable that females tend to approach roaring males, but the evaluation of this possibility must await further evidence.

SUMMARY

A male *Alligator mississipiensis* (5 feet 4 inches long) was stimulated to roar in response to a tone of approximately 57 ∼, and occasionally by the first harmonic of this fundamental. Other tones ranging upwards to 341 ∼ failed to elicit roaring but did evoke behavioral changes indicating the animal's auditory sensitivity. Three smaller males did not roar, but gave evidence that the sounds were heard. Roaring was accompanied by accurate localizing responses and by the adoption of an "aggressive approach" type of locomotion; and a smaller male was attacked repeatedly when placed in the tank with the roaring alligator. Bodily changes during roaring have been described and the bearing of present observations upon reports by field naturalists discussed.

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HORN AND SCUR INHERITANCE IN CERTAIN BREEDS OF SHEEP[1]

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WARWICK and Dunkle (1939) and Ibsen and Cox (1940) have written papers devoted to the inheritance of horns (and their absence) in sheep. The present paper is a fairly extensive revision of that by Ibsen and Cox and is based chiefly on a thorough analysis of the results of Arkell (1912) and Wood (1905, 1909). Arkell, especially, gave many details which will be utilized here but which were either not interpreted or were misinterpreted. The increase in knowledge of genetics enables one to make new interpretations with a definite assurance that they fit the facts more nearly than do the older theories.

Although the results of Arkell and of Wood are extensive, they are not by any means complete enough to fully substantiate the interpretation herein presented. Sheep are being produced at most of our agricultural experiment stations, and are under the control of men many of whom are well versed in genetics. With a working hypothesis such as the one presented here, and with others like that of Warwick and Dunkle (1939), these sheepmen should be better able to collect crucial data bearing on horn inheritance in sheep. Some of the data may be obtained in routine breeding operations, and the remainder by planned crosses.

It seems reasonable to suppose that by having a complete knowledge of the mode of inheritance of horns, etc., in sheep, cattle, goats and other horned animals, one will have important facts bearing on the question of organic evolution.

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[1] Contribution No. 147 from the Department of Animal Husbandry. Most of the experimental results in this paper are from the publications of Arkell (1912) and Wood (1905, 1909). It would require too much space to show in detail how their data fit in with the mode of inheritance herein suggested. A longer paper showing this relationship has been written, and has been placed on file with the Wistar Institute, Philadelphia. The latter has kindly consented to loan this copy to those wishing for more detailed information.

Before going into detail concerning the various characters inherited, it seems advisable to describe the pure breeds that have entered into the various crosses. In the United States there are three main types of pure breeds. (1) Those in which both sexes are hornless (also called "polled"), consisting of Southdowns, Shropshires, Hampshires and, more recently, Suffolks. All are originally from England. (2) Those in which the male is horned and the female polled. The most common breed is the Rambouillet, which, in turn, is one of several making up what are called Merinos. The latter were originally Spanish, and the Rambouillets are a French variant produced by selection. (3) Those in which both sexes are horned, the male having larger horns than the female. The Dorset Horn, coming originally from England, is the most important breed of this type.

Certain variations occur within the pure breeds. In the breeds polled in both sexes, such as Southdowns and Suffolks, a small percentage of the males develop scurs (short, hornlike growths) as they grow older. No scurs are known to develop in Southdown females, but, on the other hand, a very small number has been reported in Suffolk females. For many years it was assumed that the presence of scurs was an indication of heterozygosity. The polled condition (P) is dominant to horned (p), and scurs were thought to be found only in Pp males. Disproof for this theory is found in the fact that no horned (pp) animals are ever found in purebred Southdowns, Shropshires and Hampshires. Therefore these breeds must be PP. One horned animal, reported in Suffolks, will be discussed later. It seems more appropriate to assume that scurs are due to a separate gene (Sc), which is partially sex-limited and is epistatic to P. Further details concerning their inheritance will be discussed in the body of the paper.

In Rambouillets, where the male is horned and the female hornless, two variations may be mentioned. The most common is the presence of scurs in the females. The gene (*Sr*) producing these scurs will be shown to be different from that producing scurs in polled breeds (*Sc*). The other variation in Rambouillets is the presence of the polled condition in some of the males. Warwick and Dunkle (1939) have furnished proof that this is due to the same gene (*P*) that causes both sexes to be polled in Southdowns, etc. Warwick and co-workers (1939) have also found that one of their polled Rambouillet males has scurs, even though his composition is *PP*, thus furnishing additional evidence that scurs are not the result of heterozygosis.

All Dorset Horns are horned in both sexes, and no apparent variations have been reported. There is evidence, however, that individuals within the breed differ in regard to the genes that they carry hypostatically. Such differences are demonstrated by means of the offspring obtained in crosses with other breeds. Further details are reserved for later discussion.

GENE INTERACTIONS

Warwick and Dunkle (1939) assume that the three types of breeds above enumerated differ from each other in regard to horn character by a single gene, the three genes forming an allelomorphic series. The evidence obtained thus far, however, does not preclude other explanations. The one offered here is that all sheep are homozygous for horned (*H*) and that two pairs of modifiers act on *H* to produce the three breed types. The factor pairs are *P* = polled, *p* = absence of *P; Hm* (dominant to *hm*), *hm,* a modifier which causes an otherwise horned female to be hornless. *P* is assumed to be epistatic to *H*. Thus a *PPHHHmHm* (or *hmhm*) would be polled in both sexes, as is the case in Southdowns. A *ppHHHmHm* would be horned in both sexes (as in Dorset Horned) and a *ppHHhmhm* would be horned in the males and hornless in the females, as in Rambouillets. Both theories fit the facts so far as they are known at present. It would be necessary to run carefully planned experiments before one could get definite evidence proving one theory and disproving the other. These will not be discussed here.

Except for the assumption that scurs are the result of incomplete dominance in *Pp* males, no other theory but that of Ibsen and Cox (1940) has been advanced to explain the inheritance of scurs in sheep. They assumed that one gene (*Sc*) could explain the presence of scurs both in the hornless breeds (such as Southdowns) and in Rambouillet females. A careful study of Arkell's (1912) data has since shown that a one-gene hypothesis will not hold for both cases. Each of the two kinds of scurs is due to a different gene. Thus *Sc* produces the scurs in polled breeds and *Sr* the scurs in Rambouillet females. The interaction of these genes with other genes will be given in greater detail.

The gene *Sc* is sex-limited to the extent that in polled individuals that are *Scsc* the scurs will show only in males. Thus *Sc* is epistatic to *P* in males. It is not definitely known whether or not scurs will show in polled females that are *ScSc*. Since the character is rare in such breeds as the Southdowns, in order to obtain *ScSc* females, it would be necessary for both parents to be *Scsc,* and in that case only one fourth of the female offspring would be of the required composition. Scurred females are not known in present-day Southdowns, Shropshires and Hampshires. On the other hand, in answer to a questionnaire that I sent out to a few Suffolk breeders, one replied that he had seen a Suffolk ewe with scurs. All the breeders were agreed that from 3 to 5 per cent. of the Suffolk males have scurs. If we assume that the scurred Suffolk female is *ScSc,* and that 5 per cent. of the Suffolk males are scurred (most of these would be *Scsc*), then the chances of producing a scurred female in the Suffolk breed would be approximately $.05 \times .05 \times .25 = .000625$, or about six in every 10,000 females. Since scurs occur less frequently in the males of the other polled breeds, there would be a very small chance of their occurring in the females of these breeds.

One other fact mentioned by a Suffolk breeder might be given at this time. In 1933 a ram in his flock was born which later grew fully developed horns "with a full turn around his ears." This same breeder states that Suffolks are descended from crosses between Southdowns (*PP*) and Norfolks (*pp*). Apparently the horned ram was from heterozygous (*Pp*) parents, thus demonstrating that the Suffolk has not as yet become completely homozygous for polled, in this respect differing from the Southdown and the other polled breeds mentioned.

Those who assume that scurs are the result of heterozygosis base it on the fact that in crosses between polled (in both sexes) and horned (in both sexes) breeds many of the male offspring have scurs. Some of the crossbred males have fairly long horns, and a few have neither horns nor scurs, being clean polled. Thus, if it were heterozygosis, it would be very irregularly expressed. In those crosses where the polled parent is either a Southdown, Shropshire or Hampshire, the female offspring are clean polled. But if a Suffolk is the polled parent, some of the daughters have scurs, as will be shown later in the discussion of Wood's (1905, 1909) results.

The explanation given here for the above results is that the horned parent may carry the scur gene (*Sc*) hypostatically (*ppHHScSc*). Scurs will show in the F_1 males since *Sc* is epistatic to *P*. Assuming both parents to be homozygous, the cross would be as follows:

Polled		Horned			Males	Females
PPHHscsc	×	*ppHHScSc*	=	*PpHHScsc*	scurred	polled

An analysis of Arkell's (1912) data reveals that there is a fairly sharp line of demarcation between those F_1 males that have scurs and those that have horns. The scurs are never more than two inches long, and the horns never less than four inches in length. The horns produced in the crossbred males are assumed to be due to a separate gene (*Ha*) which is epistatic to *P* and hypostatic to horns (*ppHH*). It corresponds to the *Ha* gene in cattle, described by White and Ibsen (1936). Arkell's data are not extensive enough for one to determine whether or not *Sc* and *Ha* are allelomorphic. In the present discussion, *ha,* the allelomorph of *Ha,* is merely the absence of *Ha.* The latter will express itself in heterozygous males (*Haha*) that carry *P* (*PpHHHaha*), but females of this composition will be clean polled. It is not known whether *HaHa* "polled" females (*P*-) show horns. Arkell had one F_1 male that carried both *Sc* and *Ha.* It was scurred in appearance, thus demonstrating that *Sc* is epistatic to *Ha.* The presence of the *Ha* gene in this male was shown by the fact that he sired a horned male when mated to a purebred polled female (*PP*).

Arkell's (1912) data furnish satisfactory proof that his Rambouillets carried both of the scur genes (*Sc* and *Sr*). The presence of the *Sc* gene was demonstrated by the fact that when purebred clean-polled males (*PPscsc*) were mated to clean-polled Rambouillet females (*ppHHhmhm*) some of the sons had scurs, the gene for which must have come from the mother. Thus we are forced to conclude that *Scsc* Rambouillet females are similar to *Scsc* females of the polled-in-both-sexes (*PP*) breeds in that scurs (due to *Sc*) do not show.

The scurs that do show in a Rambouillet female are caused by another gene, *Sr,* and the gene expresses itself even when the female is heterozygous (*Srsr*). Rambouillet females without scurs (but having two bony knobs on the skull) are of the composition *srsr.* Rambouillet males are typically horned, the *Sr* gene when present being hypostatic to the horned condition. By mating a Rambouillet male to scurless (*srsr*) Rambouillet females it should be possible to determine his composition in regard to *Sr.* One such male (J. K. Madsen 2886–E) in the Kansas State College flock proved to be *Srsr.* When mated to clean-polled Rambouillet females, seven of his daughters had scurs (*Srsr*) and six did not (*srsr*).

In the present discussion all sheep are postulated to be homozygous for *H,* the horn gene. Five pairs of allelomorphs have also been postulated to account for the various "horn" conditions found in these animals. Thus it should be possible to give the genotype of the various breeds, taking all the genes into consideration. Those genes that are hypostatic in a particular breed are placed within parentheses.

The purebred polled-in-both-sexes breeds, such as the Southdowns, Shropshires and Hampshires, would be of the following composition, if neither sex showed any scurs:

PPHH (*HmHm,Hmhm,hmhm*) *hahascsc* (*SrSr,Srsr,srsr*)

In the above genotype it is assumed that *Sr* is unable to express itself in the presence of *P*. If the male is scurred, the *scsc* should be changed to *Scsc*.

Horned-in-both-sexes breeds, such as the Dorset Horn would be of the composition:

ppHHHmHm (*HaHa,Haha,haha*) (*ScSc,Scsc,scsc*) (*SrSr,Srsr,srsr*)

Some Dorset Horns have been shown by means of crosses to carry *Ha* and *Sc*, but none has ever been tested in regard to *Sr*. The test could be made by mating Dorset rams to scurless (*srsr*) Rambouillet females, and mating the crossbred rams back to scurless Rambouillet ewes. If any of the females produced from this last mating had scurs, it would be a fairly definite proof that the *Sr* gene came from the P_1 Rambouillet rams.

Purebred Rambouillets (males horned; females either hornless or scurred) would be:

ppHHhmhm (*HaHa,Haha,haha*) (*ScSc,Scsc,scsc*) *SrSr,Srsr,srsr*

Tests for the presence, or absence, of *Ha* and *Sc* can be made by means of crosses with *PP* breeds, such as the Southdown.

SUFFOLK SHEEP

Suffolks are hornless in both sexes, like Southdowns, Shropshires and Hampshires, and, like them, are of English origin. Nevertheless they are different in that they carry two dominant genes which are absent from the other three breeds. Suffolk sheep are comparatively recent importations to the United States, and have been gradually growing in popularity.

Both Arkell (1912) and Wood (1909) have reported on crosses of horned-in-both-sexes breeds with hornless-in-both-sexes breeds. Both experimenters used Dorset Horns as the horned breed, but Arkell used Southdowns, Shropshires and Hampshires as the polled breeds and Wood used only Suffolks. Wood's results were different from Arkell's and the cause seems to lie in the fact that Suffolks have certain peculiarities not found in other polled breeds.

For example, Wood (1909) and Marshall (1912) both state that scurs do not appear on Suffolk males until after they are one year old. Suffolk breeders in the United States, in answer to recent inquiries, report that 3 to 5 per cent. of Suffolk males have scurs, that some scurs appear early, and that others appear only after the animals are two years of age. Scurs when present in Southdown, Shropshire and Hampshire males always appear early. The evidence for this last statement is not complete.

The results obtained in Wood's (1909) crosses with Dorset Horns also prove that Suffolks differ from Southdowns, Shropshires and Hampshires. Wood's Suffolks apparently were scur-less, like the above breeds, but, in reciprocal crosses with Dorset Horns, the F_1 males began at an early age to develop horns. Thirty-six of the males were castrated, and their horn growth stopped almost immediately. One can not be certain that these 36 would have developed horns instead of scurs if they had not been castrated, but at any rate the two uncastrated males developed horns. These horns would be due to *Ha,* and Wood's evidence, so far as it goes, points to the fact that castration inhibits the growth of *Ha* horns. Similar results have been obtained on castration of Rambouillet rams (Nordby, 1928). In Dorset Horn rams, on the other hand, castration causes a slowing up of horn growth, but not a complete cessation. Arkell's F_1 males (Dorset Horn × Southdowns, Shropshires and Hampshires) were more variable than Wood's in that some had scurs and others, horns.

The greatest differences, however, were in the F_1 females. All Arkell's F_1 females were clean polled. All Wood's began to develop scurs in their second or third years. There were 28 F_1 females that lived to this age.

In order to explain the peculiarities within the purebred Suffolks, and also the results obtained in the F_1 and F_2 generations of crosses with horned breeds, it seems necessary to postulate that Suffolks carry two dominant genes that are not found in such polled breeds as the Southdowns, Shropshires and Hampshires. The first dominant gene (*Pe*) is one that postpones the expression in males of the scur (*Sc*) gene, but has no retarding effect on *Ha* horns in males. Before stating its effect in females it is necessary to describe the other dominant gene. This gene (*Su*) makes it possible for *Ha* to express itself in *Haha* females, thus preventing *Ha* from being partially sex-limited. It has been called *Su* because it is peculiar to the Suffolk breed. *Su-Ha-P-* females would thus tend to have horns. If *Pe* is present, however, (*Su-Ha-P-Pe-*), it delays the expression of the *Ha* gene in the female, with the result that the horns never get long, and are therefore described as scurs. It should be noted that both *Pe* and *Su* express themselves only in the presence of *P* (polled). There is no evidence concerning the effect of *Pe* on scurs in females.

Since the evidence indicates that the F_1 males and the F_1 females in Wood's crosses were uniform within each sex and, also, since the numbers were fairly large in each group, one is forced to conclude that his P_1 Suffolks and his P_1 Dorset Horns were both homozygous for a fairly large number of genes:

Suffolk Dorset Horn
(P_1) *PPHHscschahaSuSuPePe* × *ppHHSc-HaHasusupepe* =
(F_1) *PpHHSc-HahaSusuPepe* { males, horned
females, scurs appear late

In the above cross *Sc* is represented as being present in the Dorset Horns. The evidence that *Sc* was carried by at least one of the P_1 pure breeds is found in the fact that two of the F_2 animals were scurred. It has previously been shown that *Sc* is epistatic to *Ha,* and yet apparently all the F_1 males would have been horned. The reason for this is that the *Pe* gene has a delaying effect in males on *Sc,* but not on *Ha.*

Certain peculiar results obtained by Wood on backcrossing F_2 animals to P_1 can be explained by the above theory. A horned F_2 male mated to purebred Dorset Horns produced some horned offspring and one that was polled. Similar results were obtained when one of several horned F_2 females was mated to a purebred Dorset Horn. Under ordinary conditions one would expect both of the above horned parents to be recessives (*pp*), and that they thus would produce only horned offspring.

The evidence indicates that both F_2 horned animals are *PpHa-*. To explain the F_2 horned female one has to postulate that she is in addition at least *Susu* in order to permit *Ha* to express itself. She must also be *pepe,* otherwise the expression of the *Ha* gene would be postponed, and result eventually in scurs. The unexpected polled offspring from either cross would be *PpHHhahascsc* (*Susu, susu*) *pepe.*

SUMMARY

(1) All sheep are postulated to be homozygous for *H,* the gene for horns.

(2) The gene *P* (polled) is epistatic to *H.* Polled breeds are thus *PPHH* and horned breeds *ppHH.*

(3) In what would otherwise be horned animals the gene *hm* (horn modifier) causes the female to be hornless. Thus a *ppHHhmhm* male is horned and the female hornless, as in Rambouillets. Animals of the composition *ppHHHmHm* would be horned in both sexes, as in Dorset Horns. *P* is epistatic to both *Hm* and *hm.*

(4) The gene for scurs, *Sc,* is epistatic to *P,* but in heterozygous animals (*ScscP-HH*) it expresses itself only in the male. Homozygous females (*ScScP-HH*) probably are scurred. In horned animals, *Sc* is hypostatic whether it is in the homozygous or in the heterozygous condition (*ScScppHH*).

(5) Another gene for horns (*Ha*) is found in sheep. It differs from *H* in that it is epistatic to *P*. *Sc* is epistatic to *Ha*. Thus a *PpHHScscHaha* male would be scurred, while a *PpHHscscHaha* male would be horned. *Ha* apparently has no effect in a *ppHHHa*-(horned) animal.

(6) There is also another gene for scurs (*Sr*), found in Rambouillet females. It produces an effect in both heterozygotes (*Srsr*) and homozygotes (*SrSr*). Breeding tests have shown that some scurless (*srsr*) Rambouillet females may carry *Sc*, the other scur gene.

(7) Suffolk sheep, one of the hornless-in-both-sexes breeds, apparently carry two dominant genes that are not found in other hornless-in-both-sexes breeds, such as the Southdowns, Shropshires and Hampshires. The gene *Su* permits the horn gene, *Ha*, to express itself in heterozygous females (*Su-P-HHHahascsc*), thus causing *Ha* no longer to be partially sex-limited. The other gene, *Pe*, postpones the expression of the *Sc* gene in males and of the *Ha* gene in females. In *Su-Pe-P-HHHahascsc* females the expression of the *Ha* is postponed for over a year, and as a result the horns are so short that they are called scurs. In males of the same composition the horns, due to *Ha*, start growing immediately and therefore become large.

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THE SPADEFOOT TOADS IN OKLAHOMA WITH A SUMMARY OF OUR KNOWLEDGE OF THE GROUP[1]

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THE first spadefoot was described by Harlan from South Carolina in 1835. Since then, seven others have been named, all from North America, the latest in 1910. Sometimes placed in the Old World family *Pelobatidae,* they are now more commonly considered as members of a separate group, the *Scaphiopodidae,* containing the single genus, *Scaphiopus.* This paper, therefore, deals with the eight taxonomic forms of this genus.

From the first, the spadefoot toads have stimulated great interest because of several peculiarities manifested by some or all of them: (1) some species are very secretive and shy and are seldom found in numbers and then only after long intervals of time; (2) the developmental rate of their embryos and larvae exceeds that of any commonly studied amphibian (Wright and Wright, 1933; Ortenburger and Ortenburger, 1926; Trowbridge and Trowbridge, 1937; Bragg, 1941c); (3) their distribution is not what might be expected from their structure; for, having a thin, rather soft, frog-like skin suggesting an aquatic or semiaquatic habitat, all are in reality as nearly terrestrial as amphibians usually become, and most of the species are limited to xeric habitats in grasslands and deserts; and (4) the details of their taxonomic relationships have, till quite recently, been in confusion due in part to lack of specimens, in part to so few herpetologists having had opportunity to study them in their native haunts, and in part to a dearth of information on their tadpoles and life histories.

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[1] Observations on the Ecology and Natural History of Anura. XII. Contribution from the zoological laboratory of the University of Oklahoma. Aided by a grant from the Faculty Research Fund of the university and by a grant-in-aid of research from the American Association for the Advancement of Science.

With a group of species so interesting zoologically and at the same time so imperfectly known, it is understandable that false notions should have grown up about the spadefoot toads. The most notable of these is that these animals spend most of their time underground, emerging rarely except after heavy rains, breeding and then returning immediately to burrows again to await another rain. Many have accepted this uncritically, despite the fact that it leaves no obvious manner in which they could secure food.

The source of this idea is in the rarity of the solitary or hermit spadefoot of the East, *Scaphiopus holbrookii holbrookii* (Harlan), which by all accounts behaves very differently from all the other eastern frogs and toads. Ball (1936) in emphasizing the scarcity of authentic records of this species in New England points out that it had not been seen at New Haven, Connecticut, between 1879 and the time of his own studies. Concerning its breeding he adds, "in the North during the past 125 years only about sixteen instances have been recorded, all associated with heavy rains."

As the western prairies and plains became settled during the past century, other species of *Scaphiopus* were described. Almost immediately, the ideas about the rarity of the eastern spadefoot became applied to some of them. As late as 1935, I heard statements clearly implying that the plains spadefoot, *S. bombifrons* Cope, seldom emerges from the ground, and then only once a year to breed. One former Oklahoma biologist (Brooks, 1930) stated his belief that animals of this species found buried in hard-packed soil in western Oklahoma could not have emerged for several years. The finding of spadefoots (also in Oklahoma) imprisoned in balls of clay several feet below the surface under conditions very difficult to explain (Decker, 1930) may also have furthered this belief.

Those who have studied the spadefoots most carefully in their native haunts, however, have nearly always noted that they are abroad and feeding much more commonly than supposed (see Kellogg, 1932; Campbell, 1933; Ball, 1936; and others) and I have observed that some species are relatively easy to find except in hot, dry weather. I have captured hundreds of individuals of *S. bombifrons* and *S. couchii* on roads at night and have seen the latter feeding upon insects beneath street lights with garden toads of two species. On the other hand, adults of *S. hurterii* Strecker have been found only during and immediately after rains and their juveniles rarely except on moist ground.

The truth seems that some species (*e.g.*, *S. h. holbrookii* and *S. hurterii*) are more difficult to find than others (*e.g.*, *S. bombifrons*, *S. couchii* and *S. hammondii* Baird). Part of this no doubt is the result of a real difference in the habits of the two groups (see beyond) but some of it is due to the fact that the first group tends to dwell among trees, whereas the second prefers open lands. All species, so far as known, feed above ground at night and none of them spend most of their time below the earth's surface under the usual conditions of their respective native habitats. The generalization that spadefoots as a group seldom emerge from underground burrows is, therefore, without foundation in fact.

For seven years, I have studied the habits and distribution of the spadefoot toads in Oklahoma and have made more limited observations in New Mexico (Bragg, 1941c). I have seen hundreds of breeding congresses and have made detailed notes of breeding sites, breeding dates, behavior of the adults while breeding, feeding and moving about, noting the breeding calls of adults and the structure and behavior of tadpoles at all stages. I have watched metamorphosis in several species both in the laboratory and in the field. In many parts of Oklahoma, trips at night during times of breeding have been taken to find out, by following the calls, just what relation there might be between relative numbers of this or that species in one ecological community and another adjoining one.

During the earlier parts of this study I was often accompanied by my friend and former colleague, Dr. Charles Clinton Smith, who has also observed practically everything new recorded here and has greatly aided my understanding of the spadefoots through informal discussions. So closely have Dr. Smith and I worked together that it is quite impossible to separate his observations from my own even if either he or I wished to do so. This paper was originally planned as a joint contribution, but circumstances have intervened which make impossible Dr. Smith's checking my interpretations of our common efforts. For this reason, it has seemed wiser to us both to publish under my name alone and for me to assume complete responsibility for the conclusions drawn.

At the beginning of this study, *S. couchii* was the only spadefoot about which there was no question, taxonomically. *S. hammondii, S. intermontanus* and *S. bombifrons* were much confused: *S. multiplicatus* was questionably distinct from *S. hammondii: S. h. holbrookii, S. h. albus* and *S. hurterii* were similarly confused. Tadpoles of *S. hammondii, S. bombifrons, S. couchii* and *S. h. holbrookii* had been described, but an unfortunate mishap had confused those of *bombifrons* with those of *hammondii.* At the present time, due to the efforts of several investigators the tadpoles of all except the still questionable *S. h. albus* are known and the general distribution of the species within the genus is fairly well understood. Tadpoles of *S. h. holbrookii* and *S. couchii* were described by Wright (1929); those of *S. bombifrons* by Wright (1929) under the name *hammondii* (see Bragg, 1941); those of *hammondii* by Smith (1934) under the name *bombifrons;* those of *intermontanus* by Tanner (1939); those of *multiplicatus* by Taylor (1942) and those of *hurterii* by Bragg (1943). The general range of each species in the genus was approximately mapped by Tanner (1939) from specimens which he had seen, but recent work indicates some general extensions to be necessary, *e.g.,* Carl's (1942) recently finding *hammondii* in Southern British Columbia. Similarly, records of *S. couchii* in western Oklahoma (Bragg, 1941a) and new records published herewith of *S. hurterii* in the Arkansas Valley of southern Osage County, Oklahoma (Fig. 5) place these species farther north than formerly reported.

The breeding behavior of *S. bombifrons* has been reported by Trowbridge and Trowbridge (1937), Bragg (1941c) and Bragg and Smith (1942); something about that of *S. couchii* by Ortenburger (1926); that of *hammondii* by Gilmore (1924) (who also had specimens of *bombifrons* in his collection of tadpoles), Goldsmith (1925) and Bragg (1941b, c); that of *S. h. holbrookii* by several investigators, most recently by Ball (1936); and that of *S. hurterii* in notes by Smith and Leonard (1937) and Bragg (1943). The breeding behavior of *S. h. albus, S. intermontanus* and *S. multiplicatus* each still await study by any one favorably situated to observe them.

Because of the rapid advance in the study of the biology of the spadefoots in recent years, it has seemed wise to me, while reporting specifically my own observations in Oklahoma, to include a summary of all our knowledge to date about the natural history and ecological relations of these interesting animals and to attempt a synthesis of this as expressed as a phylogenetic tree. To do so at least has the advantage of focusing attention on problems still left unsolved, even though further observations may change somewhat the conclusions drawn here.

CLASSIFICATION

The genus *Scaphiopus* has eight known forms. Tanner (1939) separated two groups of species into two subgenera, Spea and Scaphiopus. I follow Tanner in this concept for reasons which appear further on.

- **Class Amphibia**
  - **Order Salientia (Anura)**
    - **Family Scaphiopodidae**
      - **Genus Scaphiopus**
        - **Subgenus Scaphiopus**
          - ***S. holbrookii holbrookii* (Harlan), 1835.**

S. holbrookii albus (Garman), 1877.
S. hurterii Strecker, 1910.
S. couchii Baird, 1854.
Subgenus Spea
S. bombifrons Cope, 1863.
S. hammondii Baird, 1859.
S. intermontanus (Cope), 1883.
S. multiplicatus Cope, 1863.

S. bombifrons and *S. hammondii* were long considered conspecific by many and subspecifically related by others. Smith (1934) was the first to demonstrate clearly their specific independence. This was confirmed by Tanner (1939); and I found it easy to distinguish the two on the basis of calls as well as structure of adults and tadpoles (Bragg, 1941c). *S. hurterii* has similarly been suspected to be conspecific with *S. h. holbrookii* or only a subspecies of the latter. But, according to Smith (1937) and confirmed by Tanner (1939), the skulls of the two are so different as to make them specifically distinct. Recently I have had opportunity to study the breeding behavior, metamorphosis and tadpoles of *S. hurterii* (Bragg, 1943) and found that these all differ in detail from those of *S. h. holbrookii* as described by Ball (1936) and others. I therefore concur with Smith and with Tanner in considering these distinct forms. *S. intermontanus* has not commonly been recognized as distinct from *S. hammondii*, which it seems closely to resemble. I have not personally seen this form, but according to Tanner (1939) its skull and other characters, as well as its tadpoles, are different from those of the latter. *S. multiplicatus* of Mexico is little known, but Taylor (1942) has shown its tadpoles to differ materially from those of *hammondii* and concludes that if the tadpoles of the latter have been correctly designated by me (Bragg, 1941b) then *multiplicatus* is specifically distinct from *hammondii*. As stated earlier *S. couchii* has always been recognized specifically, but *S. h. albus* of southern Florida is still a questionable form (Wright and Wright, 1933) although recognized by Stejneger and Barbour (1939).

As now understood, adults and tadpoles within Scaphiopus may be separated by use of the following keys.[2]

A. Adults.

1. Metatarsal tubercle elongate or sickle-shaped; parotid gland present (may be indistinct); size large. (Subgenus Scaphiopus) 2
1. Metatarsal tubercle rounded (not sickle-shaped); parotid gland absent (or present and very large in *multiplicatus*); size small. (Subgenus Spea) 5
2. Pectoral glands present; parotid and tympanum distinct 3
2. Pectoral glands absent; parotid and tympanum indistinct. *Scaphiopus* (*Scaphiopus*) *couchii* Baird
3. Ratio of head length to head width approximately 18/21; back sometimes roughened but not with restricted patch of fine dark spiny tubercles just back of eyes 4
3. Ratio of head length to head width approximately 22/25; dorsum mostly non-tuberculate except for a characteristic patch of small, dark, short spines immediately behind the eyes. *Scaphiopus* (*Scaphiopus*) *hurterii* Strecker
4. Color brown to light green, usually not particularly light-colored. *Scaphiopus* (*Scaphiopus*) *holbrookii holbrookii* (Harlan)
4. Color lighter with ''great amount of white on back, flanks, and upper surface of limbs; vermiculated irregular white bands.'' *Scaphiopus* (*Scaphiopus*) *holbrookii albus* (Garman)
5. Interorbital osseous boss present. *Scaphiopus* (*Spea*) *bombifrons* Cope
5. Interorbital osseous boss absent 6
6. Frontoparietal fontanelle present 7
6. Frontoparietal fontanelle absent. *Scaphiopus* (*Spea*) *intermontanus* Cope
7. Skin quite tuberculate on back, with several folds; head Bufo-like, short and thick; tibial gland present. *Scaphiopus* (*Spea*) *multiplicatus* Cope
7. Skin mostly smooth or only slightly tuberculate; no folds on back; head longer; tibial gland absent. *Scaphiopus* (*Spea*) *hammondii* Baird

B. Tadpoles[3]

1. Size large; color light to medium grey or brown, never very dark; shape rounded and full-bodied. (Subgenus Spea) 2
1. Size small; color very dark grey or very bronzy, sometimes nearly black. (Subgenus Scaphiopus) 5
2. Jaws with a prominent beak in upper and corresponding notch in lower; jaw-muscles well developed. *Scaphiopus* (*Spea*) *hammondii* Baird

[2] Modified from Tanner (1939) and Bragg (1942c) and extended by use of the data of Taylor (1942) and Ball (1936) on tadpoles and of Cope (1889) on adults of *multiplicatus*.

[3] Tadpoles of *S. h. albus*, still unknown.

2. Jaws with no prominent beak and notch; jaw-muscles not overdeveloped 3
3. Anterior of body much more depressed than posterior; appearance from above somewhat angular (Taylor, 1942, pl. 2, Fig. 3). Labial formula 4/4, the 1st upper row very short and across midline.
Scaphiopus (Spea) multiplicatus Cope
3. Anterior of body not much more depressed than posterior; appearance from above rounded; labial formula not 4/4, or if so, then the lowest row of teeth, rather long 4
4. Color alive, coppery; labial formula 2/4, the first upper row long and continuous except for a slight interruption in the middle.
Scaphiopus (Spea) intermontanus Cope
4. Color dark to light grey, never coppery; labial formula 4/4, 3/4 or 5/4, lowermost row of teeth long.
Scaphiopus (Spea) bombifrons Cope
5. Ground color coppery bronze with golden spots or sheens and much iridescence; labial formula 4/4, 2/4, 5/4, 3/6, or 5/5, the 1st two labial rows discontinuous, the last two continuous.
Scaphiopus (Scaphiopus) couchii Baird
5. Ground color dark grey to almost black, no dorsal iridescence or sheen 6
6. Labial formula variable (6/6, 6/5, 5/6, or 5/5), only the first two rows complete.
Scaphiopus (Scaphiopus) holbrookii holbrookii (Harlan)
6. Labial formula 4/5 or 3/4 with some variability dorsally. Only lowest (ventral) labial row typically complete.
Scaphiopus (Scaphiopus) hurterii Strecker

DISTRIBUTION

The home of the spadefoots is in the Southwest. Only *S. holbrookii holbrookii* and *S. h. albus* have spread any great distance eastward. *S. hammondii, S. intermontanus* and *S. couchii* are confined to quite xeric habitats in short-grass plains and deserts. *S. bombifrons* occurs here also, but extends eastward in the mixed-grass prairies of southwestern United States. *S. hurterii* is known only from woodlands and mid-xeric savannahs in Texas, Oklahoma and Arkansas.

Because Oklahoma is moist and low in the southeast and high and dry in the west, particularly in the northwest, and because its geographic position is almost central for possible dispersal of spadefoot toads, no area of comparable size exists more suitable for learning the ecological requirements of these animals. Extensive studies have shown the spadefoot toads here to be quite strictly limited in accordance with the ecological divisions. (For a detailed description and map of the ecological divisions, see Bragg and Smith, 1943; see also Fig. 1).

There are four species in Oklahoma, two (*hammondii* and *bombifrons*) in the subgenus Spea; the others (*hurterii* and *couchii*) in the subgenus Scaphiopus. Figs. 2 to 5 show their county distributions as now known. It is to be especially noted that *hammondii* has been taken only in the northwest, its eastern limit of distribution being in Woods County (Smith, 1934) practically coinciding with the broad ecotone between the short- and mixed-grass prairies.[4] It is especially interesting, however, that I have failed to find this species in southwestern Oklahoma, although it is here that the short-grass plains extend farthest eastward. On the other hand, *S. couchii* (a species also restricted to short-grass plains in Oklahoma)

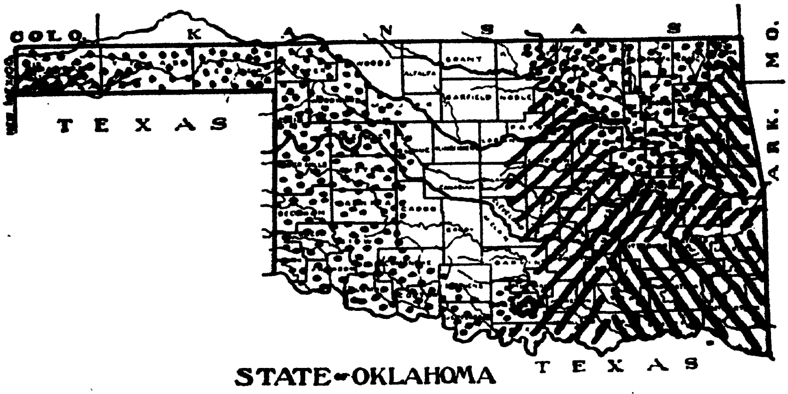

FIG. 1. Generalized ecological map of Oklahoma. Data from Bragg and Smith (1943) q.v. for more detailed map. Stipple = tall-grass prairie in northeast, short-grass plains in west. //// = Oak-hickory savannah. \\\\ = Oak-hickory-pine woodland. Unmarked = mixed-grass prairie.

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[4] The record of *S. hammondii* Baird in Payne County (Ortenburger, 1927a) is based upon a specimen of *S. bombifrons* Cope. I suspected this on ecological grounds and therefore asked Mr. C. H. Pope, of the Field Museum, to check on the identity of the specimen. His letter, dated November 31, 1941, confirms the identity as *S. bombifrons* Cope. Through the courtesy of Dr. Edw. H. Taylor, I have seen the specimen reported by Smith (1934) as *S. hammondii* from Woods County and confirm the record as of *S. hammondii* Baird.

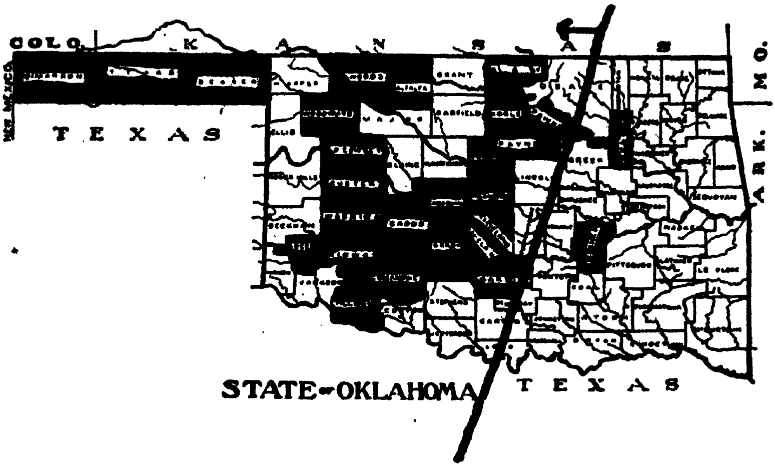

FIG. 2. County distribution of *Scaphiopus bombifrons* Cope in Oklahoma from specimens examined and literature records. The diagonal line indicates the approximate eastern limits of abundance. All records east of this are from limited local populations in prairie-islands in the savannah.

has been found *only* in the southwest, ranging eastward within this ecological community to central Stephens and Jefferson counties in the south, but only to southern Caddo County farther north. Its northern extension within the short-grass plains goes into southern Custer County, but it has not been taken north of this even at the most favorable times. This strongly suggests that *S. couchii* has recently extended its range northward, per-

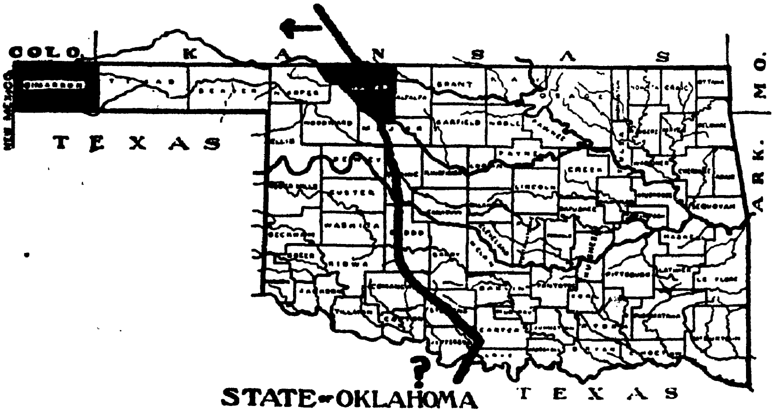

FIG. 3. County distribution of *Scaphiopus hammondii* Baird in Oklahoma. All records from the literature.

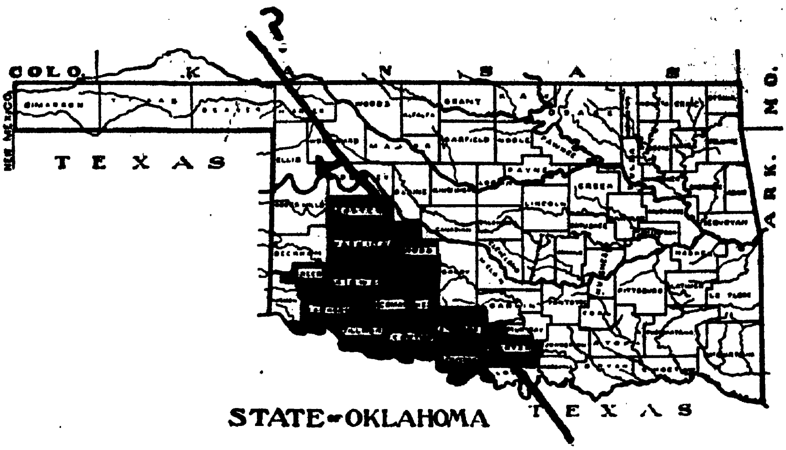

FIG. 4. County distribution of *Scaphiopus couchii* Baird, in Oklahoma. All from specimens personally examined.

haps during the recent dry phase of the climatic cycle which apparently ended with the summer of 1937.

S. bombifrons is the most widely distributed and most abundant of its genus in Oklahoma. It occupies the short-grass plains of the west and south, but is extremely abundant in the mixed-grass prairies of central Oklahoma and is also present east of this in islands of prairie in the woodland-savannah, at least to Hughes and Tulsa counties (Fig. 2). Just as *S. couchii* in western Oklahoma is

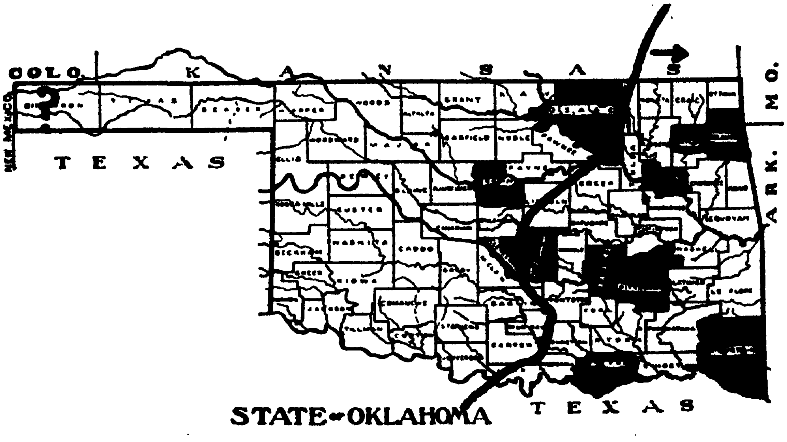

FIG. 5. County distribution of *Soaphiopus hurterii* Strecker in Oklahoma ? = record of *S. h. holbrookii* (Harlan) by Ortenburger and Freeman (1930) thought probably to be *S. hurterii* (see text).

distributed much as *Bufo compactilis* Wiegmann (Bragg and Smith, 1943), so *S. bombifrons* is distributed with *Bufo cognatus* Say. So close are these correlations that we are reasonably sure in predicting the presence of either of these spadefoots in any habitat in Oklahoma where the corresponding Bufo is found. As with *Bufo cognatus* (Bragg, 1940) *S. bombifrons* is most abundant in higher areas of the grasslands and does not enter woodland proper nor extensive flood plains at all. For example, I stood one night after a heavy and violent rain on the flood plain of the Canadian River in western Cleveland County, listening to the calls of practically all the species of frogs and toads present in the region. Calls of *S. bombifrons* reached me as a continuous roar from the prairies on either side of the river, some from congresses over two miles distant as later determined during the same night. But not a single *S. bombifrons* was seen or heard on the flood-plain, even though all the flood-plain inhabiting species were in chorus from sloughs of several types on the plain. Comparable observations were made on the Cimarron River in Logan County by Dr. Charles C. Smith and by us together on the Washita in Garvin County and by me at various other points on the Canadian and North Canadian rivers through several seasons.

S. hurterii has formerly been reported from Oklahoma only a very few times, usually as *holbrookii* (Smith and Leonard, 1934; Smith, 1937; Bragg, 1940b; 1942a). During 1941 it bred successfully in many places in eastern Oklahoma[5] and is now known to be quite abundant in all the woodland and savannah areas (Fig. 5). Except in Oklahoma it is known only in western Arkansas (Smith, 1937) and the eastern part of Texas. Comparison of Fig. 1 and Fig. 5 will reveal an apparent inconsistency, for county records are shown on the latter which seem not to conform to the ecological situation implied by the former. This is because *S. hurterii* tends to follow the flood plains of the larger streams westward where their flood-plain forests interdigitate with the grasslands. They have been found on the Arkansas, Cimarron, Canadian and Red rivers west of their general range as indicated by the line passing through Fig. 5, but just how far westward they extend is uncertain. During the period when this species was commonly considered as *S. h. holbrookii,* Ortenburger and Freeman (1930) reported the latter in the western tip of the panhandle near the Cimarron River. I have not been able to locate the specimens upon which this record is based, but I strongly suspect that they had *S. hurterii* (as also did Smith, 1937). Assuming this to be the case, *S. hurterii* may be expected in any part of Oklahoma along the larger flood-plains, but generally distributed only in the woodland and savannah in the eastern half of the state.

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[5] I am indebted to Dr. A. P. Blair for all records in northeastern Oklahoma here reported. The remainder are from specimens collected myself or sent to the University of Oklahoma Museum of Zoology. For permission to report the latter, I am indebted to Dr. A. I. Ortenburger.

HABITS OF THE SPADEFOOT TOADS

As with most animals, the habits of the spadefoot toads center about three major activities: (1) protection, (2) feeding and (3) reproduction. I give below a summary of my observations on these, principally in Oklahoma.

Spadefoots are protected from death from drying by their nocturnal and fossorial habits. All are nocturnal, most of them strictly so, although *S. bombifrons* at all ages in captivity may quickly come to the surface during daylight and may feed if it should rain or if the ground be sprinkled liberally. I have kept a number of them for more than a year in a large box to observe their reactions and have seen them hopping about in this in cool, moist, spring weather. I have never succeeded in finding them active in nature in the daytime, however, except while they were breeding, and then only a few times. During midsummer the animals in the box could seldom be induced to emerge from the soil, even by a liberal wetting with a garden hose.

To determine the relative resistance to drying, I placed twelve adult *S. bombifrons* with a comparable number of each of three species of Oklahoma Bufo (*B. cognatus, B. w. woodhousii* and *B. americanus americanus*) in a large box of moist sand indoors where they lived for several weeks. (It is to be remembered that *B. cognatus* is much like *S. bombifrons* in its ecological requirements, that *B. a. americanus* is a woodland and savannah form in Oklahoma, and that *B. w. woodhousii* occurs in nature to some extent in habitats occupied by each of the others.) All these emerged regularly at night to feed upon beetles which I placed in the box; and all behaved normally. Then I allowed the moisture gradually to evaporate in the dry air of the laboratory. Within three days of the time when the surface of the sand appeared to be thoroughly dry, no *Scaphiopus,* no *B. a. americanus* and only a few *B. cognatus* emerged at night, although most of the *B. w. woodhousii* continued to come up regularly. As the sand became drier, none appeared above the surface and after three weeks, when I judged that most of the moisture had disappeared, I dug into the sand. All the animals were found at the extreme bottom of the box. All the *B. a. americanus* and all but two *Scaphiopus* had died, and these two were thin and weak. Two of the smaller *B. cognatus* and one *B. w. woodhousii* were also dead. From this it would seem that *S. bombifrons* is less tolerant than the garden toads of its natural habitat to lack of moisture and more comparable to the toad of the woodlands and savannahs.

In a larger box kept out of doors, there were seventeen adult *S. bombifrons* with forty-four juvenile *B. cognatus* and one adult *S. couchii.* The spadefoots had lived here through two summers and winters, feeding upon insects attracted by a light placed above the box. Occasionally, the earth was dug away carefully to determine the nature of the underground burrows made by the animals. There was nothing distinctive about those made by any of them. The animals simply backed into the earth as far as they were inclined to go and remained there. When the earth was moist, all merely covered themselves, some of the garden toads even remaining with their heads protruding throughout the day. Whenever it became drier and the air hotter, all dug more deeply and emerged less frequently to feed, in extremely hot dry weather in midsummer not emerging at all. At all times there was a clear positive correlation between the tendency to dig down (and also how deeply the animals dug) and the dryness of the air and soil. There was also a correlation between the placement of the burrows and objects available near or under which they could be formed. When the ground was bare, most specimens burrowed around the edges of the box and only a few nearer its center. During three summers, when the box was left undisturbed for several weeks, plants sprouted and grew in the soil. Under these conditions about half of the burrows were close under the plants and all but two or three of the remainder still near the sides of the box. I could find no difference between *S. bombifrons* and *B. cognatus* in these things, except that *B. cognatus* emerged under drier conditions in the daytime than *S. bombifrons*.

Correlating these experimental findings with field observations, one can conclude that (1) both of these prairie species tend to be nocturnal, the spadefoot more so than the toad; (2) both form burrows the depth of which is correlated with lack of moisture; (3) both tend to emerge quickly after rain (or artificial wetting simulating a storm), the toad more quickly than the spadefoot; and (4) both tend to bore into the earth beside objects (usually plants) where (a) the ground may be softer, (b) it is more shady, and (c) the burrows are not easily observed.

Field observations indicate that there is an interspecific difference in some of these matters among the spadefoots. *S. couchii* has been found out feeding in large numbers when it was much too dry to expect *S. bombifrons*. On the other hand, *S. hurterii* has rarely been seen except during and after rain. Juveniles of this species have been found a few times feeding along dry roads on cool nights in spring (May) and autumn (October) and one very young *S. hurterii* (not more than a month from metamorphosis) was taken along a moist, shaded run in the daytime, in June. This, incidentally, is the only specimen of any spadefoot toad which I have ever found active in nature in daylight, except in breeding congresses, and except at and immediately after metamorphosis.

Virtually nothing is known about the predators molesting *Scaphiopus* and I have learned nothing during this study. Many *S. bombifrons* and *S. couchii* and some *S. hurterii* are killed during moist weather by cars on roads, especially near pools during breeding activities. *S. bombifrons* has been noted to have a sticky, musty-smelling, mucoid secretion of the skin, often exuded in some amount when the animal is handled. Whether or not this is protective, I do not know.

The feeding habits of adult spadefoot toads are closely comparable to those of the garden toads, as I have observed through several years of study of both. I have never known either to attack a vertebrate although I have had very tiny toads (*Bufo*) and young of *Scaphiopus, Rana* and hylids with adults of *Scaphiopus bombifrons, S. hammondii* and *S. couchii* and with garden toads on many occasions. Individuals of all these species, as well as of *S. hurterii,* are very adept at catching arthropods and they seem to have little discrimination (except for size) among types of insects and spiders. I have seen adults of *S. bombifrons* capture flies, hymenopterans, moths of several families (Saturniidae, Noctuidae, Notodontidae and others), beetles (Carabidae, Cincindellidae, Chrysomellidae and Scarabaeidae), bugs of several kinds, including pentatomids, and miscellaneous spiders. Young juveniles of *S. bombifrons* and *S. hurterii* feed readily upon many kinds of small insects and arachnids (Trowbridge and Trowbridge, 1937; Bragg, 1941, 1943), although the former seems to learn some food selection by trial and error.

The food of spadefoot tadpoles is of special interest. Most kinds of North American tadpoles are said to be primarily vegetable eaters, although it is well known that those of most garden toads and of the frogs do eat dead animal matter, including dead specimens of their own kind, as well as small animals taken incidentally with algae or plant debris. In contrast, many kinds of spadefoot tadpoles tend to be carnivorous and some of them show marked cannibalistic tendencies. If a piece of liver be placed in a dish containing large tadpoles of *S. bombifrons* or *S. hammondii* the animals attack it fiercely, shaking it violently (for all the world like a puppy with a slipper) and chewing out pieces to swallow. Similarly, if the smaller tadpoles of *Bufo* are placed with those of *S. bombifrons* they disappear rapidly. If one *Scaphiopus* tadpole becomes injured, the others immediately attack it, tear it to pieces and, with *S. hammondii* at least, and perhaps also *S. h. holbrookii* (Ball, 1936), they sometimes do not wait for an injury before the attack. Tadpoles of *S. hurterii* and *S. couchii* also will eat meat, but I find no record of cannibalism in these species. It should be carefully noted, however, that Trowbridge and Trowbridge (1937) found that a completely meat diet was not adequate for normal development of *S. bombifrons* and I have confirmed it for this species as well as observing it consistently in all other Oklahoma species, both in pools and in laboratory cultures.

(*To be concluded*)

NATURAL SELECTION AND THE BIRTH-RATE[1]

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WITH regard to his theory of natural selection, Darwin said "the expression often used by Herbert Spencer of 'the survival of the fittest' is more accurate, and is sometimes equally convenient." Had Darwin's foresight been equal to his understanding, he would have professed conversely that Spencer's expression is more convenient and is sometimes equally accurate, for to-day "the survival of the fittest" is a household term used to denote no more than the personal survival of those individuals most fit to endure in the struggle for existence, a definition inadequate for natural selection. More comprehensive but also incomplete as a definition of natural selection is the interpretation of "the survival of the fittest" to be the tendency for the racial survival of those inheritable factors that promote personal survival. Natural selection, however, is not only the personal survival of those fittest to survive, nor is it only the racial preservation of those genetic factors that promote personal survival. Also subject to the selective process are the inheritable factors that affect the reproductive proclivity of the organism, and that, solely as such, are causally unconnected with the traits of the individual influencing its personal survival. For instance, the prolificacy that characterizes the parasitic existence—a single human tapeworm, *Taenia saginata,* producing as many as one billion fertilized eggs during its lifetime—is a cumulative result of the selective process that, while possessing positive survival value, does not promote the viability of the individual, *i.e.,* it does not increase the individual's chance of survival.

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[1] Contribution from the Chesapeake Biological Laboratory, Solomons, Md.

Genetic factors increasing the rate of birth tend to be perpetuated by natural selection for the same reason that hereditary factors favoring personal viability are likely to be preserved, namely, that the variants they characterize are more prone to leave descendants (likewise bearing these factors) than are the not-so-modified competing types. However, the racial survival of a genetic factor, whether a determinant of personal survival or a determinant of reproductive capacity, is dependent upon the combined effectiveness of the fertility and the viability of the genetic type it characterizes. For example, a genetic factor conducive to personal viability may fail to be perpetuated if it causes an inadequate reproductory rate, or is genetically linked with factors detrimental to the fertility of its carriers. The vigor of plant and animal hybrids which is frequently unperpetuated because of concomitant sterility serves as an illustration. Similarly, inheritable factors that increase the birth-rate may not have positive survival value if they occasion a lessening of the individual's chance of survival. As an illustration, factors increasing the production of eggs beyond the ability of the parental birds to hatch and feed their progeny generally have not been perpetuated by natural selection, since they result in a retributory reduction in the viability of the offspring.

In a like manner, inheritable modifications unfavorable to the personal survival of the individuals in which they occur may have a selective advantage, if they induce a compensatory rise in the birth-rate or are genetically linked with factors that augment the rate of natality. The relatively high fertility of the feeble-minded, and some of the sexual behaviors of the lower animals, *e.g.*, mating scents, calls and colorations, which, while lessening the chance of their personal survival, increase the frequency of their cohabitation, are exemplifications. Similarly, genetic modifications that lower the rate of reproduction may be preserved, if they are associated with a compensatory gain in the individual's chance of survival. The evolution of internal embryonic development and the evolution of the intellectual faculties comprise such modifications. While they have diminished the prolificacy, these evolutionary developments have conferred a compensatory increase in the viability of the progeny (culminating in man, whose lifetime fertility is of the sparingly low value of less than three births per parental pair in the United States, but of whose offspring the strikingly high ratio of approximately 80 per cent. survive until the end of their reproductive span).

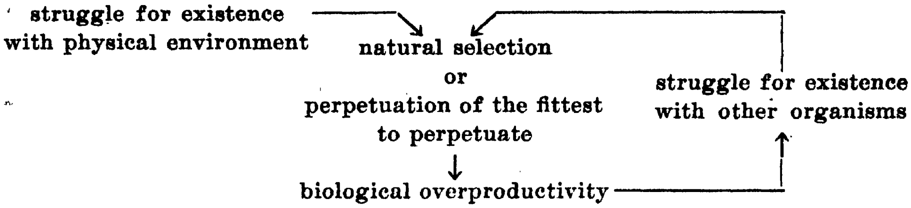
The racial survival of genetic factors that affect the birth-rate and the racial survival of genetic factors that affect personal survival are dependent upon both the fertility and the viability of the genetic types these factors characterize. Perhaps better than by Spencer's phrase with its existing ambiguity, natural selection may be defined as "the perpetuation of the fittest to perpetuate," which connotes the fitness of the individual for reproduction as well as for personal survival, and also the tendency for the perpetuation of genetic factors that impart either or both of these qualities to the individual.

Because of its overcrowding, resulting from its greater productivity, a variant with a fertility-favoring mutation eventually suffers a loss of viability, *i.e.*, it suffers a decrease in the individual's chance of survival. On the other hand, a variant with a viability-favoring mutation, *per se*, need not later undergo a loss of fertility. Instead, as its population pressure mounts, its viability more likely will be reduced to that of its not-so-modified ancestor. Since fertility-favoring mutations generally lower the individual's chance of survival, while viability-favoring mutations, *per se*, do not reduce the fertility, there is a tendency for natural selection to result in an increasing birth-rate and a consequently decreasing viability.[4]

The perpetuation of viability-favoring modifications that are directly associated with a reduction of fertility, however, has caused the reproductory rate to undergo decreases in some lines of evolutionary development.

Such are the modifications that increase the vitality of the eggs, embryos or young at the expense of the number produced, *e.g.*, an increased supply of yolk and internal embryonic development. More generally, however, natural selection results in a growing birth-rate, and, because of the increasing overproductivity, a consequently diminishing viability. This has given rise to a fertility in many organisms that is of a magnitude disproportionate to the environmental adequacies and that results in a superabundance of offspring. For example, the lifetime fertility of the big tree, *Sequoia gigantea,* is a figure that would tax the imagination, yet in a stationary population an average of only one of the millions of seeds produced by a single individual survives to the age of the parent. Such fertility results in an enormous and a generally useless mortality of pre-adult stages. Nevertheless, an otherwise superfluous rate of reproduction may be entirely useful to some species during repopulation, following the decimation caused by seasonal or fortuitous environmental changes or following dissemination to a new environment.

Darwin deduced, from the principle formulated by Malthus (1803)—"the constant tendency in all animated life to increase beyond the nourishment prepared for it," —that this biological overproductivity is the cause of the struggle for existence and thus of natural selection (Darwin, 1859). As has been previously indicated to the converse, however, the process of natural selection, which has increased the fertility beyond the environmental adequacies, is the cause of biological overproductivity. While the interorganismal competition, which results from biological overproductivity, constitutes a part of the struggle for existence, the physical conditions of the earth engender a struggle for existence with the physical environment and impose a directly selective action upon each new variation before it meets with organismal rivalry. As is indicated in the following diagram, biological overproductivity is the result, and only secondarily a causal factor, of natural selection.


struggle for existence with physical environment
natural selection or perpetuation of the fittest to perpetuate
struggle for existence with other organisms
biological overproductivity

In opposition to the occurrence of mutations, which constantly augments the variety of hereditary characters, natural selection tends to decrease the variability within a species. In addition to natural selection, there is another process that tends to decrease genetic diversity, which consists of the loss to the race of genetic factors through the process of segregation. In sexual reproduction, one member of each pair of genes possessed by either parent is ordinarily lost to each offspring because of the segregation of homologous genes in the reduction division. Due to such random loss, newly acquired mutations, whether beneficial or unfavorable, may not become established in the race, and established genes, even though they possess a survival advantage, may be reduced in frequency to the point where they are eliminated (Dobzhansky, 1941).

The chance of loss of parental alleles to the mature filial generation and hence to the species is generally independent of the birth-rate of the species, since, while the chance of loss of parental factors to the filial generation at birth is diminished by a greater fertility, the individual offspring's chance of maturation is usually commensurately decreased by a greater rate of reproduction. However, if the genetic factor confers a very large selective advantage, there may be less chance of its loss to the mature filial generation and to the species the greater the birth-rate of the species. With a higher rate of reproduction, more offspring will receive the favorable allele, and hence, if its selective advantage is sufficiently great, a larger number of favorably modified offspring will survive to maturity.

As representatives of the opposite extremes of reproductive capacity, man and the oyster can be used to illustrate the effect of the size of the birth-rate on the loss of such favorable mutations through segregation. A female human is unlikely to produce more than thirty offspring in a lifetime, and, at the prevailing rate of reproduction, would actually produce fewer than three. There is a sizable chance that a favorable mutation not present homozygously in both human parents would be lost to the race, regardless of its selective advantage, because of its failure to appear in any of the comparatively small number of offspring produced. A single female oyster, *Ostrea virginica,* on the other hand, is capable of producing several hundred million progeny. The chance of loss to the race of a beneficial parental gene because of its failure to appear in such a large filial generation at birth is insignificant. While it is inconceivable that a single mutation, or any combination of genetic factors, would confer a selective advantage enabling all the favorably modified oyster offspring to survive to maturity, it is probable that certain genes would confer a selective advantage great enough to enable the production of considerably more than three adult progeny per parental pair, which is the limit of man's reproductive ability at his prevailing rate of reproduction. If the genetic factor confers a sufficiently large selective advantage, the chance of its loss through segregation will vary inversely with the reproductory rate of the species.

Generally speaking, the later in ontogeny such favorable genetic modifications exert their selective advantage, the greater will be the chance of their loss to the adult population. The later the mutation is expressed, the smaller is the number of progeny to which it was transmitted that are still surviving at the time it confers its selective advantage, and the less is the chance that any of the favorably modified offspring will survive to maturity.

Since the perpetuation of a race is dependent upon its fertility as well as upon its viability, species with a continually declining fertility are eventually eliminated from the evolutionary procession. The subsiding birth-rate of man apparently is due to a growing hesitancy to procreate, coupled with an extending knowledge of contraceptive methods (Pearl, 1939), but, whatever the cause, a continued decrement of his rate of reproduction will result in his eventual extinction. Until man's realization of the relationship between copulation and procreation, it is unlikely that the prenatal desire for offspring possessed survival value, and consequently was not subjected to the selective process. During this period, natural selection freely intensified man's urge for personal survival, an urge that later became deterrent to his desire to bear offspring. With his eventual realization of the copulation-reproduction relationship, the inherited instincts of self-preservation became manifested in his intentional repression of procreation, a procedure that has its origin in prehistoric times (Carr-Saunders, 1922).

Although the discommodiousness of children has always existed and, except for interims such as the current war, is in general diminishing, apparently, during the last half century, man's subjective evaluation of his necessities, as reflected by his attenuating birth-rate, has been outgaining his increasing provisions. This is presumably an intensified manifestation of the survival urge, produced by relatively recent cultural changes.

The modern distending acquaintance with the methods of birth control is also a major cause of man's attenuating rate of birth, and, when this knowledge has reached a saturation point, it will not of itself cause a further contraction of his rate of reproduction. Further decline of the human birth-rate will then depend upon a continuing disproportionate increase of man's subjective standard of living. Since this has negative survival value, and since, with man's improving viability, his fertility is increasingly subjected to the selective process, it is likely that the natural selection of fertility-favoring factors eventually will become manifested in a gradually expanding rate of birth. It is presumed that the increasing birth-rate will be controlled for the welfare of humanity, and not regulated solely by the demands of the individual or for the ambition of the nation.

Inheritable factors that elevate the rate of reproduction and that, unless causing a correspondingly large reduction in the viability of their possessors, have been and will be further preserved and intensified through the processes of mutation and natural selection, may be placed in biological, psychological and sociological categories. The biological factors may be subdivided into those that augment the number of offspring in a single birth and into those that amplify the frequency of birth. Multiple ovulation, multiple development of a single zygote, and other inheritable factors conducive to multiple birth comprise the first category. Among the biological characters that amplify the frequency of birth are a prolonged period of viability of gametes; an extended reproductive span, spreading in both directions and involving fitness for survival until loss of reproductive ability; less prenatal mortality and maternal mortality of childbirth; and other improvements in the structural and functional processes of reproduction.

The two major psychological factors increasing the frequency of birth, which if inheritable have been subject to intensification by natural selection, are the desire for sexual intercourse, lending an evolutionary support to Freudian psychology; and the prenatal desire for children, dating from the time of man's realization of the connection between copulation and reproduction. Prospective sociological changes amplifying the frequency of birth, our social heritage also being subject to the selective process, are an increasing social security, social encouragement of young marriages and large families, and disapprobation of the single and childless states.

Because of the expanding usage of birth-control measures, the subjection of the desire for sexual intercourse to the action of natural selection is diminishing. This is also true of several of the biological factors that affect the birth-rate. By the same token, the sociological factors affecting the rate of reproduction and the psychological factor of the desire for children are becoming increasingly disposed to the selective process.

The recent birth-rate spurt in the United States was presumably a manifestation of the desire for children that had been provoked by impending war-engendered circumstances, *i.e.*, sexual isolation and unnatural death. When these war-born conditions transpired, they made it impossible for many to reproduce, and resulted in a resumed declination of the reproductory rate in the United States. After the Global War, the human birth-rate will continue its general decline unless and until the aforementioned social changes become effective in reducing the application of birth-control measures.

RECAPITULATION

(1) Natural selection may be defined as the perpetuation of the fittest to perpetuate, which connotes the perpetuation of genetic factors that increase fitness for reproduction as well as of those that increase fitness for personal survival.

(2) Because of the overcrowding resulting from fertility-favoring mutations, such mutations generally lead to a reduction in the viability, *i.e.*, the individual's chance of survival, of the modified types. While viability-favoring mutations that directly reduce the fertility have occurred in some lines of evolutionary development, viability increases, *per se*, do not usually result in a lowering of the fertility. Thus, there is a tendency for natural selection to result in a growing birth-rate and a consequently decreasing viability.

(3) Natural selection is the direct cause, and only secondarily a result, of biological overproductivity.

(4) Chance of loss of very-favorable genetic factors through segregation varies inversely with the repro-

ductory rate of the species and directly with the extent of individual development at the time the selective advantage of the factor is expressed.

(5) Man's diminishing birth-rate is due to a spreading knowledge of contraceptive methods, coupled with a growing hesitancy to procreate, the latter being a recently intensified manifestation of the urge for personal survival, an urge that was excessively enlarged by natural selection before the prenatal desire for children became subjected to the selective process.

(6) Since the expression of man's survival urge in the renigment of reproduction has negative survival value, intensification by natural selection of inheritable biological, psychological and particularly sociological characters that increase the birth-rate should eventually result in an increasing rate of reproduction.

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THE NATURALIST IN AMERICA IN 1942 ± 75 YEARS[1, 2]

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IN those regions of the western hemisphere that had developed a high degree of autochthonous civilization, such as those of the Nahuas and Mayas of Mexico and the Incas of Peru, for example, a knowledge of nature had developed very fully before the arrival of the Europeans, and, looking back at our continental past, it is there that we should be able to find the first American naturalists.

Although traces of the knowledge of nature in the original cultures have remained for us in their monuments, and although a few final sparks could still be seen during the first few years of European domination, as, for example, in the magnificent herbal organized in 1552 by the Indians, Martin de la Cruz and Juan Badiano, nevertheless, one can say that on the whole the intellectual development of the primitive Americans in those regions in which they reached a high level was interrupted abruptly with the introduction of European culture.

In 1570, there arrived in New Spain the eminent Francisco Hernandez, private physician to Philip II, who sent him to study the plants and animals of the colony, and who Reed (1942) assumes "was probably the first botanical expedition sent out by a government." With Hernandez, who was afterwards called "the Pliny of New Spain," there began on our continent four centuries ago the era of naturalists of European orientation.

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[1] This paper was prepared for the annual meeting of the American Society of Naturalists, which was scheduled to be held in New York City on December 29, 1942, but was cancelled owing to war conditions.

[2] The writer feels very much indebted to Dr. José Zozaya, for criticism of the manuscript, and to Dr. and Mrs. William Vogt, also for critical reading of the manuscript, as well as for translating to English the Spanish original.

Slowly, along with the advance of European colonization, the study of nature progressed, but it is not really until the eighteenth century that we can speak of "American naturalists," in the United States as well as in the rest of the countries of this continent.

In the United States, as Kofoid says, there was "an indigenous biology springing from the soil, field and forests and assisted in part by the dependence of medicine upon biology. The biologists of the American tradition were naturalists interested in the flora and fauna of the New World. The names of Catesby, Audubon, Bachman, Halbrock, Bartram, Rafinesque, Say, Isaac Lea and many others adorn the pages of biological history in the earlier years."

In Mexico, at about the same time, there were the Spaniards, Sessé and Cervantes, and the Mexicans, Alzate and Mociño, together with Bustamante and others, who started the Mexican school of natural history that, as Kofoid observed in the United States, was by preference concerned with the study of plants and animals with a marked interest in the medical applications of these studies. Especially was this true in the field of botany, in which the Mexican school was heir to the extensive Aztec knowledge of medicinal plants. The initiation of these studies followed a similar path in the rest of the hemisphere, at about the same time, as we can see in the work of Mutis in Colombia, Molina in Chile, Azara and Muniz in Argentina, etc. One must not forget, however, the profound influence on American science exercised by that illustrious traveler, Alexander von Humboldt.

We can say then, as might be logically expected, the first inspiration of the students of our hemisphere was the knowledge of the animals, plants and minerals that existed in it. And this state of things was the one that still prevailed up to seventy-five years ago, up to the last third of the nineteenth century.

These last seventy-five years have seen, all over the world, a profound change in the point of view of the men dedicated to the investigation of nature. With the consistent use of the microscope, begun in its modern form about the middle of the eighteenth century, with the perfection of physics and chemistry that offered their apparatus and reagents to facilitate the study of living creatures, the biological laboratory was born, with the character that it has had during the last hundred years, and thanks to whose work the life sciences have progressed to a remarkable degree.

Unfortunately, in certain sectors there arose also an unjustified conflict between those scientists who followed the old methods of natural history in its classical form, especially in the field and in the museums, and those who were taking the new trails of experimentation.

The veteran North American zoologist, L. J. Cole (1941), sums up this situation in a graceful article reviving youthful memories:

> Where our graduate group worked there was an iron grill which separated the museum from the zoological laboratories. It separated almost as effectually the ''species spliters'' from the ''sperm chasers.'' . . . The field naturalist and museum worker felt that the ''closet zoologist,'' as he dubbed the laboratory investigator, was working under such artificial conditions that its findings had little relation to animals in ''natural'' surroundings. Above all, that he had little conception of taxonomic problems, and the chances were that if he should meet in the wild the animal on whose tissues he was working he would not recognize it. The embryologist, physiologist or cytologist on his part accused the taxonomist of playing a game about on a par with arranging a collection of postage stamps, and of splitting genera into species, and species into subspecies, merely for the doubtful distinction of getting his name attached to the specimens and embalmed for posterity and for eternity along with them.

These conflicting points of view became so accentuated in later years that with the great success of the experimental laboratory sciences the rest of the departments of natural sciences were to a certain extent neglected.

Such an attitude, world wide, was undoubtedly one-sided, and very soon voices were raised in warning against the danger that was being run in abandoning the classical methods of natural history, not only because of their own objective value, but also because of their close relationship with the experimental work of the laboratory to which their findings offer a great deal in the way of points of departure for other investigations.

Twenty years ago, in 1923, Professor Ashworth in his address as president of the Section of Zoology of the British Association for the Advancement of Science, commenting on what he felt to be the state of the animal sciences then, said:

> The danger that morphology will be pushed to excess is long past; the peril seems to me to be rather in the opposite direction, *i.e.*, that some of our students before passing on to research receive too little of that training and discipline in exact morphology by which alone they can be brought to appreciate how the components of the living organism are related to one another and to those of allied species or genera, and how they afford, with proper handling, many data for the evolutionist. I plead, therefore, for the retention of a sound and adequate basis of morphology in our zoological courses. . . . Another of the basal supports of our science an appreciation of which or better still a training in some branch of which we must encourage is the systematic or taxonomic aspect. The student or graduate who is proceeding to specialize in experimental zoology or genetics particularly requires a sound appreciation of the fact that the accurate determination of the genus and species under investigation is a primary requisite for all critical work, it is part of the fundamental data of the experiment and is essential, if for nothing else, to permit subsequent observers to repeat and perhaps to extend any given series of observations.

The situation pointed out in England in 1923 appeared to be the same in the United States even in 1938, when Professor F. R. Lillie, referring to the future of the zoological sciences wrote:

> There is a strong tendency among zoologists at the present time, especially those devoted to experimental methods, to believe that these subjects (taxonomy, comparative anatomy, paleontology, embryology and geographic distribution) have played their main role already in the development of zoology; and so in many places these fields of zoological education are neglected. The consequent failure, where such a situation exists, to appreciate the richness and interrelationships of animal life, the perfection of adaptations and the immensity of time in the geological ages that have gone into their creation is a grave defect in the education of the zoologists. . . . The basic descriptive disciplines of zoology are, moreover, live subjects for research. The background is occupied by the descriptive and systematic observational disciplines, which need and continue to receive constant attention, if only in the service of experimental investigators which require increasingly exact observational bases.

And this interesting opinion of Lillie's, even more interesting coming from an individual so well versed in and acquainted with laboratory techniques and methods, is the same that Crocker expresses, referring to the future of botany, in an article published the same year, 1938:

> Finally, the conditions met in a laboratory are limited and principles established in the laboratory need to be tested and modified as to limitations and breadth of significance by tests under the more varied conditions in the field and in nature.

In the above quotations we have tried to make evident a point of view with respect to the modern orientation of the natural sciences that appears to be universal, since Ashworth and many other scientists in Europe have expressed the same opinions as have Lillie, Crocker and many more in America.

However, since the aim of this paper is to concern itself especially with the role played by the naturalists of our continent, it may be well to state something that in our opinion explains the prejudice that has been noted in the natural sciences of America, to some extent, against field and museum studies.

We said at the beginning of this paper that with the arrival of the European conquerors and colonizers in the sixteenth and seventeenth centuries, the aboriginal civilization of America among those people who had succeeded in developing any, was abruptly cut off and replaced by that imported from Europe, especially from England, France, Spain and Portugal, nations that played the preponderant part in the formation of the present American countries, and that besides were centers of European culture of that time.

Now in Europe the methodical study of flora and fauna had already been initiated by the Greek and Roman scientists—Aristotle, Theophrastus, Pliny and many others; later, during the long period of the Middle Ages, new contributions, although in small numbers, were being made in these fields. And about the dawn of the Renaissance and during its prime, especially under the influence of men such as Ray, Linnaeus, Tournefort, Gesner, Aldobrandi and many others, there arose a veritable furor for the systematic knowledge of the flora and fauna of little Europe, a knowledge that by the beginning of the eighteenth century was well under way. Each country could rely on acceptable catalogues of its plants and animals more or less correctly classified.

So that when with the beginnings of the nineteenth century the biological laboratory got its vigorous start, thanks to the patient early work of the naturalists, European students already had the indispensable morphological and systematic base from which to take off for their new experimental explorations.

In America the situation was different. With the aboriginal culture interrupted, and the European culture transplanted here during the sixteenth and seventeenth centuries, we received Europe's scientific knowledge in its current state, it is true, but we did not receive nor could we have received the preliminary work of centuries during which it had become established.

On a continent many times larger than Europe were implanted the advanced methods of the biologists, in their many aspects, without there having been previously fulfilled the basic and fundamental requirement of a systematic classification of the fauna and flora.

It is very interesting to note that Kofoid, in the article to which we referred before, speaks of the influence that French thought exercised in the United States, especially through Franklin, Jefferson and Agassiz, who was a disciple of Cuvier; of the influence of German thought through the many young Americans who went to round out their studies in the famous laboratories of Leuckart, Boveri and many others; and of the English influence, particularly with the coming of Huxley to Johns Hopkins, as well as through Osler and others. Now these were the currents that vitalized and succeeded in establishing on the brilliant foundation on which later we have seen it develop, the experimental and laboratory work of modern North American biological science. But Kofoid speaks also of the naturalists in the American tradition interested in the flora and fauna of the New World. It was precisely the Catesbys, the Audubons, the Rafinesques and their kind who, for the most part unconnected with universities or official institutions, felt least the influence of European thought, and in consequence began their work following the biological path that had been traversed centuries before by their colleagues of the Old World, and that even up to to-day, in all the Western Hemisphere with its immense area, and most especially in the Latin American countries, we have only just started on.

Consequently the conditions created in Europe by the flowering of experimental and laboratory work, although extremely fertile, had however as a lamentable corollary, a certain neglect of the classic basic disciplines of natural history—a neglect which on our continent has been even more acute, not only because of the greater extent of our territory and the consequent richness and variety of our flora and fauna, many times greater than Europe's, but also, and perhaps more important, because we did not have the advantage of the work of earlier generations of naturalists who in Europe were collecting and classifying plants and animals during a period in which European civilization did not even exist in the New World, or had barely achieved a foothold through the bloody struggle of the conquest, and the precarious events of colonial days.

The present struggle in which our countries are engaged has demonstrated how little we know of the natural history of our continent. When it has been necessary to send soldiers into strategic zones, at times practically unexplored and uninhabited, vital and urgent questions have arisen: What animals and plants are found there? Which are useful and which might be injurious? What do we know of their biology that might orient us in their utilization and control? Occasionally information can be found in libraries and museums to clear up these mysteries; frequently no information at all can be obtained and it is necessary to begin research at once, regretting that at the proper time sufficient emphasis was not laid on this kind of investigation, that some people, perhaps, might have considered "antiquated."

The war has pointed up also, with unusual emphasis, the vital value of nature conservation in all its phases. And this work requires unavoidably a previous knowledge and an adequate description and classification of the resources to be conserved.

In our opinion, the classic work of the naturalist in the basic descriptive disciplines still holds an indisputable place in the study of nature throughout the world " . . . if only in the service of experimental investigators which requiere increasingly exact observational bases," as Lillie says.

But on the American continent the demand is even more urgent for a larger number of naturalists to study its seas, investigate its rivers and explore its jungles and mountains. The catalogue of our plants and animals has hardly been started, and it is vitally necessary that it be completed not only for the benefit of those scientific investigators that would discover its endless finds to be a great interest in clearing up different biological problems, but also from the point of view of its practical use.

In fact, many American countries whose diet is deficient can find through the systematic exploration of their flora and fauna new sources of food to improve the popular diet.

Besides, progress in communications, with the daily use of the automobile and airplane, represents a potential danger in the transportation of disease vectors, whose distribution can only be known adequately after exploring all corners of the hemisphere.

Because of the emphasis that we have laid on the basic disciplines of the natural sciences, which, in our point of view, have been quite unjustly forgotten, it might be thought that we underestimate the experimental work of the laboratory, since we have said nothing in its defense. Nothing is further from our thoughts. If we do not raise our voice in favor of the laboratory, it is because we feel that it needs no defense, since what the experimental studies have done in the past for the advancement of the natural sciences is so well known and so justly esteemed, as well as are the great things that may be expected of them in the future.

Since by preference we have been occupied personally in laboratory work, we could not advise the abandonment or neglect of such study; on the contrary, we know its value and believe that it should be furthered as much as possible. Nor are we considering a return to the Linnaean era, which, in the present state of the natural sciences, would result in sterility. But we do believe that it is necessary to preserve a due respect for the field work and museum work of the ''naturalist'' *sensu strictu.*

The growth and progress of science have always been cumulative and cooperative. Each investigator who honestly tries to wrest one of her secrets from nature, whatever the end he pursues or the methods he employs, makes a useful contribution. The contribution may be of such character that its theoretical importance or its practical applications are immediately apparent, and no one will deny its value. At other times the data obtained, for a thousand extrinsic or intrinsic reasons, appear to be without any importance, condemned beforehand to oblivion. However, if the result was arrived at honestly and is consequently reliable, however small it may appear it will be an element that later will enter into the construction of larger theoretical concepts or will be useful in achieving some practical end.

There is no need, therefore, in our opinion, to try to evaluate in hierarchial form that which each branch of the natural sciences can contribute to the total knowledge of nature, and to the control, direction and utilization of nature for the benefit of man—an end that has always been the goal towards which the masses of humanity have moved since the moment, lost in the darkness of time, in which our most remote ancestors began to know, and later to organize their knowledge of those things mineral, vegetable and animal that might profit them, or, on the contrary, that might harm them.

From an abstract point of view, all the branches of the natural sciences are equally useful as techniques for knowing nature. In isolation, it is possible that not one of them may be considered complete or perfect. Together, they complement each other; each one makes its own contribution, that, linked with that of all others, will make possible the building up of an overall picture of nature.

In our opinion, then, one of the most important aspirations for the next seventy-five years is that of achieving a harmonious understanding among the different branches of the natural sciences, in such a manner that, each one working in its own special field, with its own resources, can contribute its partial findings, which, united with the rest, will serve to construct the whole that will enable us to better interpret nature.

One must not forget that if each one of the branches of the natural sciences has its peculiar problems and uses special techniques to solve them, all together they have in common the use of one basic tool—the scientific method, which, based on observation and experiment, and eliminating in consequence the prejudices and personal caprices of the investigator, governs equally the work of the morphologist and systematist as that of the physiologist and geneticist. And in all cases, if it is correctly employed it should give results comparable in biological significance, no matter what the special techniques by which they have been obtained.

Another goal to be reached in America is the achievement of better understanding among the naturalists of the whole continent, from Alaska and Canada to Argentina and Chile. In the past each one of our countries has felt a closer bond with one or more of the European countries than with its neighbors of the western hemisphere. It is still common to meet naturalists in the Latin American countries who, although well acquainted with European science, especially that of France, are practically ignorant of what the United States has done in this field, believing that in that country the spirit of the business man, the industrialist, in one word, the promoter, leaves no room for the development of scientific thought. On the other hand, not a few scientists of the United States are equally ignorant of what their colleagues south of the Rio Grande are accomplishing, and they think that in the republics of Latin origin the arts, poetry and literature, mixed with politics, are the only pursuits of the inhabitants, incapable of the rigorous work of scientific investigation.

For an American science of biology to be developed that shall be really productive and worthy of respect, we must end such a state of things. Fortunately, the necessities of the moment that to a certain extent have obliged our continent to be self-contained culturally, and that have forced thousands of scholars to explore it in all directions, are forming bonds of friendship and fellowship among the naturalists of the twenty-two Americas, who, knowing each other, are beginning to esteem each other.

The Latin American naturalist is becoming convinced that the great development of science in the United States has much to offer him, and he no longer persists in believing that all cultural inspiration must come from Europe. The Anglo-Saxon naturalists, on their part, have had an opportunity to see with their own eyes what is being accomplished, if on a more modest scale, in the Latin American countries, and with such contact with their colleagues of another language, there has been born a genuine appreciation for the work that many of them are pursuing.

Besides, and this is very important, both have become aware that in the field of natural science in its broadest meaning there exists such infinite problems of such magnitude that one country alone could never solve them satisfactorily, and as a consequence they may never be solved definitively unless every nation offers its contribution to their solutions.

With all their mistakes and limitations, the contribution of the last seventy-five years of the natural sciences on the American continent is something to be proud of. If the next seventy-five years succeed in giving their just due to each of the different branches of the biological disciplines, without distinction or preference for any one of them, much will be accomplished.

And if an effective scientific union can be achieved, a real sincere, disinterested and honest cooperation among all the naturalists of the hemisphere, from Hudson Bay to the Strait of Magellan, we can not only feel proud of the accomplishment, but we shall be able to say then that there is an American science of biology.

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REVIEWS AND COMMENTS

EDITED BY PROFESSOR CARL L. HUBBS

IN these reviews and notices of current biological publications emphasis is given to books and major articles which fall within the special scope of THE AMERICAN NATURALIST, in that they deal with the factors of organic evolution. REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, Scripps Institution of Oceanography, La Jolla, California. All opinions are those of the reviewer.

The Haplolepidae, a New Family of Late Carboniferous Bony Fishes. A Study in Taxonomy and Evolution. By T. STANLEY WESTOLL. Bull. Am. Mus. Nat. Hist., 83, 1944: 1–122, pls. 1–10, figs. 1–52. $1.75.

THIS new family is erected for one of the many phyletic lines into which the primitive actinopterygian or paleoniscoid fishes are now supposed to have evolved. The Haplolepidae were very small fishes, with large scales, greatly reduced opercular bones, few fin rays that were but slightly or not at all branched, and certain features trending toward the holostean type. The paucity of meristic parts and general structural reductions may have been related to dwarfing.

These fossils are brought so nearly into life by Westoll that they all but swim across the page. They are skillfully interpreted as having been surface-inhabiting fishes of warm marshy waters that were deficient in oxygen. Indeed I see in the restorations remarkable likenesses to the viviparous topminnows, the Poeciliidae, of similar Recent waters. The resemblances include a terminal mouth, a flattish back, a small posterior dorsal fin, and a caudal region so oriented as to remain in the water as the fish swims against the surface film. Of particular import is the occurrence in both groups, and in certain other surface-swimming teleosts, of lateral line organs on the ventral surface. Ventral lateral lines in the Actinopterygii are therefore not confined, as the author suggested, to the Haplolepidae. Since they occur in such teleosts as the Poeciliidae and certain Atherinidae, their occurrence in the Carboniferous family may not have been an archaic feature.

General remarks are included on the phylogeny of the Actinopterygii, the main line of fishes. The transition from the sharklike chondrostean type through the "Sub-Holostei" and the supposedly polypheletic Holostei to the Teleostei, involving particularly the change from a strongly heterocercal to a homocercal caudal fin, is correlated with the adoption of a marine habitat by the fishes which had previously lived in quiet fresh-waters. The modification in fin structure is related to the increased density of the environment, the lesser need of an upward driving mechanism and "the loss of the structural devices for providing 'lift'". I regard this interpretation as erroneous for the following reasons: living fishes with ordinary heterocercal tails are bottom dwellers, and nearly all are marine; motions of a heterocercal caudal would seem to produce a downward rather than an upward thrust; the adjustment in specific gravity could more readily have been made by a reduction in the air bladder. I would look on the transformation in caudal structure rather as an adaptation to provide the increased speed called for in the open waters of the newly invaded seas. Parallel changes are suggested by the pseudo-homocercal caudal of the speedy surface-swimming lamnoid sharks and of the fossil genus *Cladoselache.*

Plant Viruses and Virus Diseases. Second revised edition. By F. C. BAWDEN. Waltham, Mass.: Chronica Botanica Co.; New York: G. E. Stechert and Co., 1943: i–xi, 1–294, figs. 1–48. $4.75.

THE first edition of this book was published at Leiden, Holland, in 1939. Due to the Nazi invasion the plates were lost and the book was out of print within a year.

Until less than a decade ago, work on the viruses had been largely in the hands of bacteriologists and pathologists. Fortunately, the attention of chemists, physicists, entomologists, serologists and other specialists has been turned toward solving some of the perplexing problems of this branch of science. An inevitable result is that the publications are widely scattered in apparently unrelated journals, and in language unfamiliar to many biologists. The author of this text deals primarily with the nature of viruses themselves, and only in a general way with the diseases caused by such agents. In spite of the war, research in this field has continued to make rapid progress, thereby justifying the thorough revision and extension which is presented in the current edition. Under present difficulties the writer has succeeded admirably in bringing together the new knowledge of this field.

Chapter I surveys the general problem and includes a definition of a virus, a history of virus diseases and a review of the problem of nomenclature. The symptomatology of plant virus diseases is well covered in the next two chapters. The transmission of viruses and their relationship to insect vectors, both of which are important problems of long standing, are brought up to date in the fourth and fifth chapters. In the next chapter "virus strains, mutations, and acquired immunity" are given due consideration. The similarity and differences between immunity in plants and in animals are clearly presented, together with a thorough coverage of the botanical phenomena involved. The Serological Reactions of Plant Viruses, a subject of interest because of its bearing on the current problem of classification, is the topic of chapter VII.

Chapter VIII deals with the "purification of viruses." In the following chapter the chemical and physical properties of the purified virus preparations are considered. In the tenth chapter the author presents, in terms a biologist can comprehend, the highly technical subject of "optical properties of the purified virus preparations." Chapter XI takes up the "inactivation of viruses," a subject of importance in the description and identification of viruses. The physiology of the host plant in relation to the virus, the controversial subject of classification and the technics of disease control are discussed in chapters

XIII to XV. The need of a system of classification based upon the virus is emphasized. The writer points out the necessity of a knowledge of the virus, its host relations and methods of transmission, if sound control measures are to be devised. General control measures are briefly discussed.

In a final chapter the origin and multiplication of viruses are considered. The controversy of whether viruses are living or non-living may be unimportant, but it has aroused much interest and is well presented in these final pages. With the questions of origin, multiplication and the living versus non-living nature of viruses, the author leaves his reader to carry on.

The biologist who has not been able to follow the voluminous literature in this field should find Bawden's book a very welcome addition to his library. It gives a clear, concise, excellently illustrated discussion of most of the literature, by one who has been actively engaged in the study of the chemistry and physics of viruses. The book is beyond a doubt a significant contribution to our scientific literature.

J. ARTHUR HERRICK

NOTICES OF NEW BOOKS AND ARTICLES

The Living Mosaic. By CARL EPLING. Faculty Research Lectures, University of California, Los Angeles. Berkeley and Los Angeles: University of California Press, 1944: 1–26, figs. 1–16. $0.25.—The modern field of speciation is very interestingly presented in this lecture, by a skilful combination of generalizations and examples. Species are treated as one of the highest levels of biological organization. The interaction of heredity and variation is stressed. Geographical variation and segregation are clarified by a brief epitome of Epling's thorough studies on the pitcher sage, *Lepechinia*. Isolating mechanisms are then given emphasis, with illustrations of the types of mechanisms taken from the author's studies of sages, *Salvia*. Inferences on the past history of evolutionary lines from biogeographical data, are exemplified from Epling's recently published study of *Drosophila pseudo-obscura*.

The Ecotype. By J. W. GREGOR. Biological Reviews, 19, 1944: 20–30.—Ecotypic differentiation is defined as an hereditary change occasioned by the selective action of the habitat. Such speciation may be independent in respect to different environmental trends, and may be regional or strictly local. It is most frequent in species with wide latitudinal or altitudinal distributions. Clines correlated with gradual changes in climate comprise a limited number of distinct populations. Zones of intergraduation are usually narrow. Effects of hybridization may spread without destroying the integrity of the hybridizing forms. "Ecoclinal subspecies," with objectively delimited ranges, should be recognized nomenclatorially on the subspecies level, but "ecoclinal ecotypes," with subjectively delimited ranges of ecotypic variation, are not to be accorded subspecies names.

The Distribution of the Salamanders of the Genus *Plethodon* in Eastern United States and Canada. By ARNOLD B. GROBMAN. Ann. N. Y. Acad. Sci., 45, 1944: 261–316, figs. 1–11. $0.75.—Much of interest to students of speciation is included in this paper. Emphasis is placed on geographical equivalence, though the new term "syngeographs" for geographical equivalent or sympatric forms hardly seems needed. The terms sympatric and allopatric are also used, and it is properly pointed out that there was no warrant in my suggestion (AM. NAT., 77, 1943: 174) that these terms are etymologic hybrids and should be replaced by "compatric" and "alipatric." It is demonstrated that the ranges of the salamanders treated are closely correlated with areas of forest types, with the extent of continental glaciation and with physiographic provinces. The ranges of these animals are apparently limited by recognizable barriers. Terminal raciation is finely illustrated.

Guide to Higher Aquarium Animals. By EDWARD T. BOARDMAN. Bull. Cranbrook Inst. Sci., 21, 1944: 1–108, 60 figs. $2.00. —In characteristically attractive style the Cranbrook Institute of Science presents another of its guides to nature. It is skilfully written down and should serve effectively in introducing the local fishes, amphibians, and aquatic reptiles that can be cared for in aquaria to the youngsters of Michigan and adjacent regions, and to older folks who would stay young by cultivating a personal acquaintance with these fascinating animals.

A Review of the Halfbeaks or Hemiramphidae of the Philippines and Adjacent Waters. By ALBERT W. C. T. HERRE. Stanford Univ. Publ. (Univ. Ser.; Biol. Sci.) 9: 39–86, 1 map. $1.00.—A general account of the characteristics and natural history of this highly specialized family of synentognathous fishes precedes the revision. Most of the species belong to the viviparous genera *Zenarchopterus* and *Dermogenys*, the classification of which is largely based on the secondary sexual modifications of the fin rays in the males.

Entomology for Introductory Courses. By ROBERT MATHESON. Ithaca, New York: Comstock Publishing Co., 1944: i–xiv, 1–600, frontisp., figs. 1–500. $5.50.—Another fine book on insects comes from Cornell, the home of entomology in America. After connecting the insects, through their near relatives, with other animals, the author gives an account of insect anatomy adequate for the taxonomic study that follows, order by order. The systematic section covers more than half the pages but not so large a proportion as in some other recent texts. Families are distinguished in a series of previously tested keys. Interesting statements are included on the life histories and economic relations of important insects. Illustrations abound. The four final chapters deal in an elementary way with "Insects in Relation to Human Welfare." Glossary, Bibliography, and Index close the attractive volume.

Manual of Human Protozoa. By RICHARD R. KUDO. Springfield, Illinois: Charles C Thomas, 1944: i–ix, 1–125, figs. 1–29. $2.00.—This new book adds another volume to the already ample number of publications devoted to aiding the student or medical man interested in war diseases caused by protozoan parasites. The printing and illustrations are of the usual high order of the Thomas publications. There are, however, many mistakes of sentence construction, such as misplaced adverbs and the dropping of articles, that cause confusion in the reader's mind. Several instances of questionable descriptions of morphology are noted. The author follows the usual method of calling the parasite a commensal whenever there is any doubt regarding its pathogenicity. The directions for making permanent preparations of protozoa in fecal samples needs to be radically revised, as it is doubtful whether a student would be successful in his efforts when following these directions. Since it is confined to the important human parasites the manual will be of value to medical and pre-medical students.—A. E. WOODHEAD.

Gestation Periods: A Table and Bibliography. Compiled by J. H. KENNETH. Imperial Bureau of Animal Breeding and Genetics. Edinburgh: Oliver and Boyd, Ltd., 1943: 1–23. 2s. (orders and payments to be made to Imperial Agricultural Bureaux, Central Sales Branch, Agricultural Research Building, Penglais, Aberystwyth, England).—The data apply to mammals only, and are arranged alphabetically by English vernaculars. Average, minimum, or maximum figures are presented (all when available), with references to the 341 items in the bibliography. No appraisal of the data is offered, except for the marking by an asterisk of figures based on single cases.

Macquarie Island Its Geography and Geology. By DOUGLAS MAWSON, based mainly on the records of LESLIE RUSSEL MAWSON. Australian Antarctic Expedition 1911–14, Sci. Repts., (A) 5, 1943: 1–194, pls. 1–37, maps and figs. 1–46. 1£, 15s.—Though primarily a geological and geographic study, this report contains an account of the fauna and flora of Macquarie Island, in the Antarctic south of New Zealand, along with statements on the extinction of the fur-seals and of the ground parakeet and on the precarious status on the island of the penguins and sea-elephants. It is held to be the duty of civilization to set up here a preserve to save the interesting fauna and flora from extinction. Macquarie Island is the sole breeding ground for birds and mammals that forage over a vaste expanse of sea.

AMERICAN SOCIETY OF NATURALISTS

The American Society of Naturalists met in Cleveland on September 12–14, under the presidency of Dr. FAY-COOPER COLE. The Symposium on Biology and Human Progress was attended by about 150 persons. The program was as follows:

1. Biology and the Public Mind, Charles V. Taylor, Stanford University
2. Plants and the Material Basis of Civilization, Edmund W. Sinnott, Yale University
3. The Rehabilitation of Biological Research and Education in War Stricken Countries, Robert Chambers, New York University

There were elected to membership in the society: J. B. BUCK, University of Rochester; GEO. L. CROSS, University of Oklahoma;

MAX DELBRUCK, University of Tennessee; BORIS EPHRUSSI, Johns Hopkins University; KATHERINE ESAU, University of California at Davis; G. L. GRAHAM, Rockefeller Institute; IVAN JOHNSTON, Harvard University; D. H. LINDER, Harvard University; PHILIP A. MUNZ, Pomona College; GREGORY PINCUS, Clark University; ALBERT TYLER, California Institute of Technology; FRANZ VERDOORN, editor *Chronica Botanica.* As Honorary Members to fill vacancies there were elected: G. H. PARKER, Harvard University; R. G. HARRISON, Yale University; F. R. LILLIE, University of Chicago; all have served as President of the Society and all joined it before 1900.

As officers of the Society there were elected, as President, E. W. SINNOTT, Yale University, as Vice-President, K. S. LASHLEY, Harvard University, and as Treasurer, T. M. SONNEBORN, Indiana University. To fill three vacancies on the editorial board of THE AMERICAN NATURALIST caused by retirement under the by-law establishing the editorial board, there were elected J. H. BODINE, University of Iowa, P. W. WHITING, University of Pennsylvania, and SEWALL WRIGHT, University of Chicago.

Following the annual dinner of the society which was attended by 61 persons, the Presidential address was delivered by FAY-COOPER COLE of the University of Chicago, on "Some Problems of Human Racial Development and Migration."

WILLIAM RANDOLPH TAYLOR, Secretary

AMERICAN SOCIETY OF GENETICISTS

Secretary LAWRENCE H. SNYDER writes that there is no news to report, since the meeting of the American Society of Geneticists which was scheduled to be held at Cleveland along with the American Association for the Advancement of Science was cancelled at the urgent request of the Office of Defense Transportation.

Other affiliated societies, strong in the conviction that science is an essential element of modern civilization, did meet at Cleveland. There was fair attendance and more than usual interest was displayed, particularly in the discussions of the papers that were read.

SHORTER ARTICLES AND DISCUSSION

CRYPTIC BOBBED ALLELES IN *DROSOPHILA MELANOGASTER*

IN a short note Spencer[1] reported the following features discovered in *Drosophila hydei.* A wild population contained a complete series of multiple alleles at the bb-locus ranging from homozygous wild type to homozygous lethal alleles; the first were discovered by compound effects. The phenotype included such features as bristle length, abnormal abdominal sclerites and some other characters like viability and fertility. The different alleles could act more strongly on one or the other character differentially. There was no complete dominance. Most tested females carried two different bb-alleles.

In a series of experiments on spontaneous mutation in *Drosophila melanogaster* of which a report is now in press, facts were found which parallel more or less those indicated by Spencer for *D. hydei:*

(1) In a set of one-pair cultures from a series of our experimental stocks occasionally flies were found with etched abdomen but completely normal bristles. The insufficient chitinization of the lateral edges of the abdominal tergites (etching) is one of the usual phenotypical effects of the higher bobbed alleles and is found together with the bb-type of bristles. It turned out that the etched flies contained a bb-allele which in homozygous condition does not influence the bristles but produces etching (in a varying percentage of females). Thus among the offspring of 20 pairs of the stock pointed = svr^{poi}, etched females were found in 8 cases in the following proportions: 1 in 43, 15 in 71, 5 in 72, and 5 times most females were etched. These flies were tested with two bb stocks kindly provided by Professor Curt Stern: a low one y g bb with only a small bristle effect, and a higher one called bb-lethal carried as ClB/w^e bbl with a higher bristle effect and also producing an etching effect. The compound effects (as well as localization experiments) demonstrated that the etching in the tested flies was due to a bb-allele with no effect upon the bristles but an effect upon the abdomen. In order to save space the description of the phenotypes of these and other compounds is tabulated below (Table 1).

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[1] W. P. Spencer, *Genetics,* 23: 170, 1938.

(2) The same allele was found to be present more or less frequently in other stocks derived by mutation from an original stock called pxbl, but it also was found in a stock $svr^{pol\ h}$ of completely different origin.

(3) A similar bb-allele was found to be present in a homozygous or heterozygous condition in almost all individuals of a standard a px sp stock ($bb^{a\ px\ sp}$). Again bristles are completely normal, but a slight tendency toward etching is present. But the compound of bb^{pol} and $bb^{a\ px\ sp}$, both without a bristle effect, is slightly bobbed and the etching effect is increased. The same is true for the compounds bb/bb^{pol} and $bb/bb^{a\ px\ sp}$, while the bb-test (from y g bb) produces only a very small visible effect in homozygous condition. (See the table where the effects are separated into classes.) A still higher class of effect is produced in the compound with bbl which shows $bb^{a\ px\ sp}$ to be a higher allele than bb^{pol}. Thus the bristle effect has a threshold nearer to normality than the threshold for the abdominal effect, as seen in the behavior of the lowest alleles. But in the higher grades both effects increase roughly parallel with a certain amount of variation. The increase of both effects in the compounds of two alleles both with

TABLE 1

AVERAGE PHENOTYPE OF SOME bb-ALLELES AND COMPOUNDS AT 25° BUT NOT ISOGENIC

bb-allele		Origin		Known modifiers	Bristles phenotype	Abdomen
X^1	X^2	X^1	X^2			
bb	bb	y g bb	y g bb		± bb1	± achi 1
+	bb^1	ClB	w^e bb^1	probably present	+, some bb^s	± achi 1
bb	bb^1	y g bb	"		2–3	achi 3–4
bb	bb	y g bb	y g bb	modif. bran	+	+
bb^1	+	w^e bb^1	diff. stocks	modif. bran	+	± achi 1
bb^{pol}	bb^{pol}	diff. stocks	diff. stocks		+	± achi 1
bb^{pol}	bb	$svr^{pol\ dish}$	y g bb		1–2	± achi 2
bb^{pol}	bb^{pol}	svr^{pol}	$svr^{pol\ sq}$	modif. bran	2–3	achi 2
bb	bb^{pol}	y g bb	$svr^{pol\ sq}$	"	1–2	achi 1–2
bb^{pol}	bb^1	$svr^{pol\ dish}$	w^e bb^1		2–3	achi 2
$bb^{a\ px\ sp}$	$bb^{a\ px\ sp}$	a px sp	a px sp		+	± achi 1
"	"	"	"	"	± 1	± achi 1
"	bb	"	y g bb		1–2 (2)	± achi 2 (1–3)
"	bb^1	"	w^e bb^1		2–4 (4)	achi 3–4 (4)
"	bb^{pol}	"	svr^{pol}		1 (2)	achi 1–2
$bb^{pol\ hi}$	$bb^{pol\ hi}$	diff.	stocks		lethal	lethal
"	bb	"	y g bb		4–5 (2–4)	achi 5 (3–4)
"	bb^1	"	w^e bb^1		5	5
$bb^{pol\ hi}$	bb^{pol}	svr^{pol}	$svr^{pol\ dish}$		4–5	4–5
"	$bb^{a\ px\ sp}$	$svr^{pol\ dish}$	a px sp		3–4	3–4
"	"	$svr^{pol\ dish}$	a px sp		5	5
$bb^{a\ px\ sp\ h}$	$bb^{a\ px\ sp\ h}$	a px sp	a px sp		lethal	lethal
$bb^{a\ px\ sp\ h}$	$bb^{a\ px\ sp}$	a px sp	a px sp		4–5	3–4

Legend: classes bb 1–5 = little, ¼, ½, ¾, complete, shortening of bristles. Classes achi 1–5 = little, more etching, large patches of larval chitin, more larval than imaginal chitin, almost no imaginal chitin. + achi 1 = most flies normal, a few achi 1. ± bb = mostly normal, few beginning bb. Classes in parenthesis: different experiments subthreshold or almost subthreshold effects in the homozygote is remarkable.

(4) The abdominal effect actually consists of the persistence of larval chitin. In the lower grades this appears only at the edges of the tergites; in the most extreme grades practically no imaginal chitin is formed and the unsegmented-looking abdomen is covered with white, wrinkled larval chitin. All degrees exist between these two conditions (classes 1–5). We will call this the achi effect (from achitinous). In the a px sp stock occasionally a high achi bobbed fly is found, and once even an extreme member of class 5 appeared. This is based upon a higher allele with considerable effect upon both bristles and chitinization, the allele $bb^{a\ px\ sp\ h}$. It is dominant, homozygous almost lethal, and it considerably reduces viability and fertility in compounds so that segregating classes are too small. Flies of grade 5 can be bred only in mass culture. Males with this high allele have a tendency to possess slight deficiencies in chitinization in the genital segments (cr. 10% ♂♂) while the bristles remain normal. The compound between the two a px sp alleles is extreme bobbed. If the hemizygous males are viable the cross $bb^{a\ px\ sp}/bb^{a\ px\ sp\ h} \times bb^{a\ px\ sp\ h}/Y$ produces offspring of which one half are lethal ♀♀ and half are like the mother. Thus a high-grade achi line can be bred as if it were homozygous if the proper males are selected. The number of ♀♀ is small since one half are lethal and the other half poorly viable. There is reason to assume that the high allele arises frequently by mutation in the stock (see below).

Also from svr^{poi} which contained the bb^{poi} allele a high allele was derived which is a little lower than $bb^{a\ px\ sp\ h}$ but also homozygous lethal. This allele $bb^{poi\ hi}$ was derived from different stocks of svr-alleles, especially from those called $svr^{poi\ sq}$ and $svr^{poi\ dish}$. In this case its origin by repeated mutation could be proved as the allele appeared repeatedly in selection experiments that were closely watched.

(5) In addition it was frequently observed that in crosses involving bb, bb^{poi} and $bb^{a\ px\ sp}$ a few high bobbed achi individuals appeared among the segregating ± low bobbed achi or even normal individuals. Tests always revealed the presence of a heterozygous higher bb-allele which could have arisen by mutation, which seems to occur much more frequently at the bb locus than at any other known locus. It is as a rule discovered only when a compound effect produces the high phenotype.

(6) The test of all these alleles in different compounds reveals that their order is: bb (Stern's y g bb)—bb^{pol}—$bb^{a\ px\ sp}$—$bb^{pol\ hi}$, bbl (from Stern)—$bb^{a\ px\ sp\ h}$. There is no reason to assume that the bb and achi effects, and also viability and fertility, do not act in a parallel way, though there are threshold differences which put the achi effect frequently about one class ahead of the bobbed effect, while viability and fertility are only affected in the highest classes of those effects. An exact evaluation is rather difficult because the effects are highly modifiable, both genetically and environmentally. Thus it was found that an arc allele (called bran) increases the effect while the a px deficiency, which itself has a similar phenotype to that of bobbed, does not increase the effect. The Dichete inversion is a powerful plus modifier. Quantitative work, using isogenic stocks, is much hampered by the fact that so many stocks contain invisible alleles of bb which become visible in the experiments. Thus the Cy-inversion stock used for such experiments was found to contain such an allele. Another difficulty which affects the reliability of classification comes from the existence of modifiers for the achi pattern. Thus in the presence of the mutant $svr^{pol\ dish}$ the achi pattern loses its irregularity and follows a definite rule: in the higher grades the imaginal chitin is restricted to the central posterior edges of the tergites. (Acording to old descriptions the mutant abnormal abdomen, near the left end of the first chromosome, which is no longer available, had this phenotype. It was ascertained by localization experiments that this mutant is not involved in our case.)

(7) At the time of the discovery of bb it was found (see Morgan and Bridges 1916)[2] that hereditary bobbed males appeared occasionally, and this was interpreted as a mutation of the $+^{bb}$ locus in the Y-chromosome. We observed the same phenomenon repeatedly in bb^{pol}, $bb^{a\ px\ sp\ h}$. The responsibility of the Y-chromosome was easily ascertained in F_1, F_2, etc., of crosses of bb-males to attached-X females in which the abnormal Y-chromosomes from the bb-♂ is present in males of even generations but not present in males of odd generations with the expected results upon the phenotype of bb males. But it seems that the most obvious explanation based on a mutation in the Y-chromosome did not suffice because cases were found in which bb-achi males could not contain an X with bb, if the records were correct. But no final solution was found. (The bb-males are greatly enhanced by Dichete which

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[2] T. H. Morgan and C. B. Bridges, Carnegie Inst. Washington, Publ. 237.

produces a huge achi effect of the dorsal type described above.) Another remarkable fact, which does not agree so well with the idea of a mutation in the Y-chromosome is that males with bbl in the X plus the changed Y are normal. More work on these bb males in isogenic stocks, with sufficiently marked X-chromosomes and the use of broken Y-chromosomes is needed, as well as work with isogenic stocks of the different alleles described, comparable to the recent work of Stern[3] on ci-alleles.

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VARIATIONS IN THE OFFSPRING OF TETRAPLOID OENOTHERAS

IT is well known that the offspring of the tetraploid *gigas* mutation from *Oenothera Lamarckiana* show wide variability in leaf-width, but the nature of this variation has never been analyzed. *Gigas* mutations have appeared in several other species of Oenothera, including *O. grandifolia* described from Eastern Nova Scotia.[1] A single tetraploid of this species appeared in 1936 in the Regent's Park cultures and flowered so late that there was little chance of crossing with other forms. A culture of 35 plants was grown in 1938 from seeds of an unprotected flower. Two plants had larger rosettes than the rest. They grew into larger, taller plants and were recognized as probably triploids. They were subsequently shown[2] to have 21 chromosomes, mostly in short chains of two or three at diakinesis.

The remainder of the culture were like other *gigas* strains,

TABLE 1

Plant number	Chromosomes	Petal-length	Midleaf[a]	Stem height	Per cent. good pollen
				inches	
II. 5	28	24–26 mm	15 cm × 41 mm	30	46
II. 2	29	19 mm	10.5 cm × 28 mm	27	16
III. 1	29	....	19 cm × 42 mm	28	19
III. 5	27	19 mm	13 cm × 47 mm (waved)	39	41
II. 4	27	uprooted	....	..	..
II. 6	22	24 × 22 mm	15 cm × 21 mm	31	15
II. 8	21	16 × 13 mm	12 cm × 28 mm	24	12

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[3] *Genetics*, 28: 441–475, 1943; *Proc. Nat. Acad. Wash.*, 29: 351–367, 1943.

[1] R. R. Gates, *Phil. Trans. Roy. Soc. B*, 226: 239–355, 1936, 73 figs.

[2] G. N. Pathak, Studies in the Cytology of Oenothera, *Am. Jour. Bot.* 27: 117–121, 1940, 24 figs.

[a] This means a leaf taken half-way up the stem.

strongly biennial, and the rosettes showed wide variation in width of the leaves on different plants. Only 25 survived the winter and flowered in 1939. Material from seven of these plants was collected for cytological study. Their main features are shown in Table 1.

The wide range of variation in leaf-width in *O. Lamarckiana gigas* was formerly described and illustrated.[4] A *gigas lata* mutation presumably had 29 chromosomes, the extra one being the same as in *O. lata* with 15 chromosomes. Another derivative of *gigas* with 27 chromosomes[4a] differed in having smaller leaves and

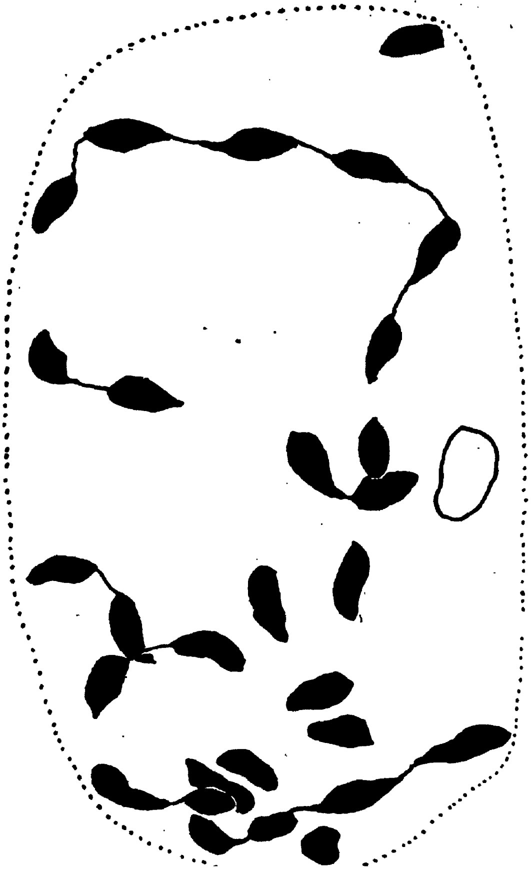

FIG. 1. Pollen diakinesis in *Oenothera grandifolia gigas*, plant with 29 chromosomes.

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[4] R. R. Gates, "The Mutation Factor in Evolution," p. 118, figs. 43–53, 1915.

[4a] Gates 1915, p. 217.

flowers and 23 per cent. of triangular pollen grains (those of *gigas* being normally quadrangular). Another plant in the same culture, with apparently 27 chromosomes, had very narrow leaves and was highly pollen-sterile.

The variability of the *O. grandifolia gigas* culture was such that it was not always possible to determine by inspection which plants had aberrant chromosomes numbers. No. II. 5 was chosen as typical because of its flower-size, leaf-width and height. Its 28 chromosomes were in chains of two or three at diakinesis, with many single ones. Nos. II. 2 and III. 1 had 29 chromosomes which were nearly all single at diakinesis in some nuclei and in chains up to 4 or 6 in others (Fig. 1). These hypertetraploid plants had smaller flowers and shorter stems than the normal tetraploids and a much higher percentage of bad pollen. They were by no means identical, however, as shown by the foliage. As appears in Table 1, one had much larger and wider leaves than the other. In a larger culture a whole series of (4n + 1) plants would be expected, but on present knowledge they can not be distinguished by their phenotypic characters from (4n — 1) mutants.

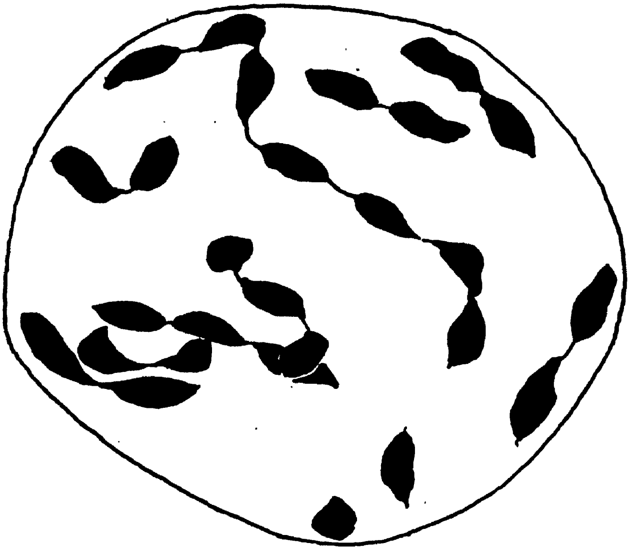

FIG. 2. Pollen diakinesis in *Oenothera grandifolia gigas*, plant with 27 chromosomes.

Plants III. 5 and II. 4 had 27 chromosomes, mostly in chains containing up to 7 chromosomes (Fig. 2). From Table 1, it will be seen that III. 5 had flowers of the same size as (4n + 1) plants,

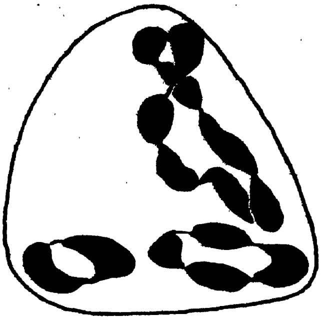

FIG. 3. *O. biformiflora* × *O. blandina*. Diakinesis showing $8+4+1_{II}$ chromosomes.

but a taller stem and a much higher percentage of good pollen. Its leaves, however, were relatively short and extremely broad. A series of (4n — 1) plants may be expected, differing in leaf-width and other characters according to which chromosome is missing.

In addition to the two annual triploids already mentioned, two biennial plants in this culture (see Table 1) had respectively 22 and 21 chromosomes. The latter had narrow, the former very narrow leaves. Even as rosettes they were conspicuously distinct. They also differed markedly in flower-size and in height, the plant with the extra chromosome being larger in both respects.

The wide variability of the various strains of tetraploid Oenothera is thus largely accounted for by the occurrence of, (a) offspring with (4n + 1) and (4n — 1) chromosomes, arising through non-disjunction; (b) offspring with 3n or (3n + 1) chromosomes. There are also (c) *gigas nanella* mutations in some strains, and (d) occasional diploids, probably of parthenogenetic origin. A complete analysis of these various phenotypes would require cultures of *gigas* on a large scale, and these are difficult to obtain, partly because of the small number of seeds produced per flower. It is clear, however, that the phenotype of these *gigas* variants depends on the particular assembly of chromosomes in each.

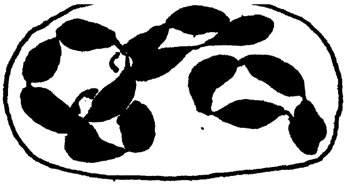

FIG. 4. *O. Victorini parviflora* × *O. blandina*. Diakinesis showing $4+4+4+1_{II}$ chromosomes.

Davis[5] has recently concluded that *gigas* mutations probably arise usually from somatic chromosome doubling in the fertilized egg, as one of us[6] originally assumed, but that they may rarely arise from a triploid through the union of two diploid gametes.

In the genus Oenothera the most conspicuous changes occurring in hyper- and hypotetraploid forms are in leaf-width, with others in size of flowers, height of stem and the proportion of good pollen. That this is not necessarily the case in other genera is shown by a 4*n* strain of *Antirrhinum majus.*[7] In this species the hyper- and hypotetraploid plants (descended from a tetraploid produced by colchicine) varied most markedly in the form and color of the zygomorphic flowers. There were also habit differences, but these are not described. The extremes in chromosome number among 274 plants ran, however, from $(4n+3)$ to $(4n-5)$.

Three new Oenothera catenations may be appended to this note. *O. biformiflora* (broad) × *blandina* has eight + four + 1_{II} (Fig. 3) *O. Victorini parviflora* × *blandina* has four + four + four + 1_{II} (Fig. 4) and *O. sackvillensis* Gates has a ring of fourteen. This work was suspended by the war.

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[5] B. M. Davis, *Genetics*, 28: 269–285, 1943.

[6] R. R. Gates, *Arch. f. Zellforsch.*, 3: 525–552, 1919.

[7] J. Straub, *Ber. deut. bot. Gesells.*, 59: 110–113, pl. 1, 1941.

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